Tesis Doctoral

El papel ecológico de los materiales orgánicos alóctonos en las comunidades de macroinvertebrados en playas atlánticas arenosas: patrones espaciales y temporales

Universidad de Cádiz
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Mª del Carmen Ruiz Delgado
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UNIVERSIDAD DE CÁDIZ
Facultad de Ciencias del Mar y Ambientales
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UNIVERSIDAD PABLO DE OLAVIDE
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Área de Zoología

EL PAPEL ECOLÓGICO DE LOS MATERIALES ORGÁNICOS ALÓCTONOS EN LAS COMUNIDADES DE MACROINVERTEBRADOS EN PLAYAS ATLÁNTICAS ARENOSAS: PATRONES ESPACIALES Y TEMPORALES

THE ECOLOGICAL ROLE OF WRACK DEBRIS FOR MACROINVERTEBRATE ASSEMBLAGES ON ATLANTIC SANDY BEACHES: SPATIAL AND TEMPORAL PATTERNS

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Memoria presentada por **Mª del Carmen Ruiz Delgado** para optar al **título de Doctora** con mención internacional por la Universidad de Cádiz

Esta memoria ha sido realizada bajo la dirección de: Dr. Francisco José García García y Dr. Juan Emilio Sanchéz Moyano

Lda. Mª del Carmen Ruiz Delgado
Aspirante al Grado de Doctora
Cádiz, noviembre 2014

Dr. **Francisco José García García**, Catedratico de Zoología de la Universidad Pablo de Olavide y Dr. **Juan Emilio Sánchez Moyano**, Profesor Titular de Zoología de la Universidad de Sevilla

CERTIFICAN

Que los trabajos de investigación desarrollados en la memoria de tesis doctoral titulada: "**El papel ecológico de los materiales orgánicos alóctonos en las comunidades de macroinvertebrados en playas atlánticas arenosas: patrones espaciales y temporales**" han sido realizados bajo nuestra dirección en el Area de Zoología de la Universidad Pablo de Olavide y son aptos para ser presentados por la Lda. **Mª del Carmen Ruiz Delgado** ante el Tribunal que en su día se designe para aspirar al Grado de Doctora con Mención Internacional por la Universidad de Cádiz.

Y para que así conste, y en cumplimiento de las disposiciones legales vigentes extendemos el presente certificado a 14 de noviembre de 2014.

Dr. Francisco José García García

Dr. Juan Emilio Sánchez Moyano

Dr. **Alejandro Pérez Hurtado de Mendoza**, Profesor Titular de Zoología de la Universidad de Cádiz

CERTIFICA

Que los trabajos de investigación desarrollados en la memoria de tesis doctoral titulada: "**El papel ecológico de los materiales orgánicos alóctonos en las comunidades de macroinvertebrados en playas atlánticas arenosas: patrones espaciales y temporales**" han sido realizados bajo su tutela y son aptos para ser presentados por la Lda. **Mª del Carmen Ruiz Delgado** ante el Tribunal que en su día se designe para aspirar al Grado de Doctora con Mención Internacional por la Universidad de Cádiz.

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Dr. Alejandro Pérez Hurtado de Mendoza

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Let´s Wrack and Roll!

(A mi familia y en

especial a mi Jose)

GENERAL ABSTRACT

Accumulations of seagrass, macroalgae and other organic materials, collectively known as wrack, commonly occur on sandy beaches worldwide, and are critical to the functioning of these ecosystems. On the upper beach, the deposition of wrack debris provides habitat and food for rich supralittoral macrofauna of crustaceans and insects, which cannot be found in any other environment and play key roles in the ecosystem functioning. Despite this, the removal of wrack debris is a widespread practice on sandy beaches, and there is little information regarding the effects of such wrack removal on associated macroinvertebrates. The general aim of this thesis is to evaluate the spatio-temporal variation in the distribution and utilization of wrack debris by supralittoral arthropods and its biological responses to wrack removal, which, in turn, is relevant to the management of this key resource (i.e. wrack debris) on sandy beaches.

We investigated the influence of the spatial distribution and the relative ageing of upper wrack deposits on the composition and structure of macroinvertebrate assemblages on six sandy beaches located at Brazilian and Spanish Atlantic coasts (**Chapter 1**). We found that, independently of the wrack composition, the spatial distribution of wrack deposits at different tidal levels (i.e. bands) on the upper beach influence the structure of supralittoral assemblages. Bands wrack play a role shaping the density of dominant taxa (i.e. Talitridae, Tenebrionidae and Staphylinidae) on Atlantic sandy upper shores. In the **Chapter 2**, the abiotic factors that could influence the distribution of supralittoral arthropods was analysed in relation to the deposition and location of wrack debris at two Spanish Atlantic beaches. We found differences in the community structure and composition between microhabitats (bare and wrack-covered areas), due to the influence of wrack deposits on the habitat selection by arthropod species. The labile organic matter (BPC) combined with temperature or moisture mostly explained the distribution pattern of assemblages. Changes of these habitat features in relation to the ageing of wrack debris play an undeniable role in the utilization of wrack by supralittoral arthropods, and therefore, in the spatial distribution of species between wrack bands. These results provided evidences about the role of algal wrack structuring assemblages (diversity and composition) of supralittoral arthropods.

The colonization process by supralittoral arthropods at naturally strandlines was investigated in the **Chapter 3**. For this, we manipulated the presence of stranded wrack and then monitored the wrack-associated fauna after the stranding of new wrack debris

on the Atlantic upper beaches (southern Brazil and south-western Spain) for a 47-day period. Our results showed that naturally stranded wrack debris can be promptly invaded by a wide range of colonizer species (i.e. talitrid, dipterans, tenebrionids, staphylinids, and spiders) that indicate high heterogeneity of habitat and/or food sources available for supralittoral arthropods in natural driftlines. Moreover, the results demonstrated that the colonization of strandlines was slower in southern Brazil (16-day period) than in south-western Spain (3-day period). This process was driven by changes in the densities of Talitridae, Staphylinidae, and Tenebrionidae species in both regions. Moreover, beetles of Cleridae and Nitidulidae also contributed to colonizer community in southern Brazil (Paraná region). The dynamics of wrack supply, the species-specific adaptations (i.e. mobility) and strategies to use wrack debris (as refuge and/or feeding site) could explain the different colonization patterns of assemblages in both Atlantic regions.

The direct effect of wrack removal on the community structure and composition was analysed using a manipulative experiment, where we evaluated the biological responses before and after to remove all organic debris detached at the Atlantic upper shores (**Chapter 4 and 5**). We found that a short-term wrack removal resulted in detectable changes in the density of some species, mainly talitrid amphipods, and therefore in community structure, but these was rapidly recovered, although the timing of recovery was more protracted for supralittoral assemblages of southern Brazil than did of south-western Spain. The temporal variability of wrack biomass and the specie-specific adaptations of invertebrates inhabiting strandlines might determine the response of the supralittoral assemblages to wrack removal on beaches located at both sides of Atlantic Ocean.

This thesis increases our knowledge concerning the interaction between wrack debris and supralittoral macroinvertebrates, highlighting the role of stranded organic materials in shaping communities as shelter, breeding and/or feeding sites. Moreover, the results of this study demonstrate that the removal of wrack debris affect the structure and composition of supralittoral assemblages. Therefore, wrack debris should be considered a key component on sandy beaches because it provides habitat and food for supralittoral macroinvertebrates, forming islands of biodiversity which support coastal food webs. The conservation of wrack debris and the reduction of human impact on associated fauna are crucial to maintain the functional integrity of beach ecosystems.

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GENERAL INTRODUCTION

GENERAL INTRODUCTION

➢ Sandy beaches as a complex system

Sandy shores constitute some of the most extensive intertidal systems, making up two-thrids of the world's coastlines (Bascom, 1980; McLachlan and Brown, 2006). Open-coast sandy beaches predominate in tropical and temperate regions (Davis and Fitzgerald, 2004). They are estimated to represent between the 11% and 34 % of the coastline (Short, 1999). These unique ecosystems are iconic assets to society, since they provide a wide range of services to meet human needs across many dimensions: economic support, provision of living space and food, recreation, cultural and spiritual fulfilment, and protection against destructive natural events (Schlacher et al., 2007; Schlacher et al., 2008). While the economic and social values of beaches are generally regarded as paramount, sandy shores also have special ecological features that is generally not recognized (Schlacher et al., 2007; Defeo et al., 2009). Beaches are thus far from the ecological deserts of popular belief. Rather, they harbour unique and diverse suites of species not found in any other marine habitat (McLachlan and Brown, 2006; Schlacher et al., 2008; Defeo et al., 2009). Beaches are a unique environment occupied by invertebrate species that have adapted to the constant motion of sand (McLachlan and Brown, 2006; Schlacher et al., 2007), and in addition, provide habitats for many wildlife species (birds, amphibians, reptiles, fishes) which nest, breed, feed, and rest on coastal dunes or the open beach (Dugan et al., 2003; Schlacher et al., 2007; Defeo et al., 2009; Schlacher et al., 2014). Moreover, sandy beaches play and important role in coastal ecology and dynamics, linking the fauna and processes of sand dunes, the surf zone, intertidal zones, and nearby rocky reefs. Therefore, beaches are socio-ecological systems where physical, ecological, and socio-economic factors interact in a complex way. Consequently, the assessment of ecological state of sandy beaches is a hard task, but necessary in order to achieve appropriate management and successful conservation of beach ecosystems (McLachlan and Brown, 2006).

- *The physical environment*

Beach systems consist of wave-deposited accumulations of sediment on the shore, complicated by the presence of tides and variable sediment, each of which influence beach morphodynamics and behaviour (McLachlan and Brown, 2006; Short and Jackson, 2013). Waves provide the driving force of most physical, chemical, and

biological processes in these systems. Wave behaviour and its interaction with the sediment determine the cross-shore beach profile (Fig. 1). The surf zone is the most dynamic part of the beach, owing to the energy released by breaking waves and morphology containing single and multiple long-shore and transverse bars, troughs, and channels. The swash zone is where waves collapse on reaching the shoreline and flow up onto the beach as laminar swashes, maintaining a relatively steep beach face slope. The highest boundary of the beach is the limit of the swash during spring tide. This zone comprises the upper limit of the swash and the highest boundary of the beach and is called subaerial zone (Fig. 1) (Short, 1999). Eventually, there is a spray zone that is never covered by water and belongs to the upper part of the beach normally forming part of some type of dune system. This environment is also known as the supralittoral or subterrestial zone.

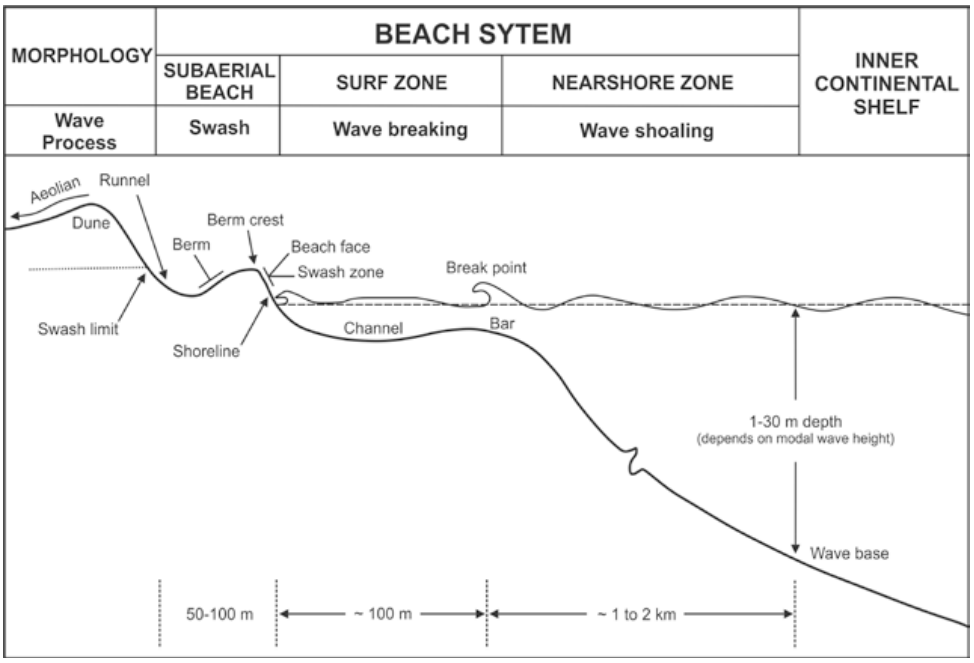

Figure 1.Features of a high energy beach at mid tide. Modified from Short (1999)

Sediment size and sorting contribute to the overall beach gradient and type, with fine sand maintaining a low gradient swash zone and a wide and dissipative surf zone. With increasing grain size, the beach face will steepen and the surf zone will narrow. Tides are a component of most beaches and, although these are not required for beach formation, they can have considerable impact on beach morphodynamics (McLachlan and Brown, 2006). Tides shift the shoreline both horizontally and vertically. In areas within the high-tide range, the tidal variation in nearshore water depth can also

determine breaker-wave height by increasing wave shoaling at low tide. At higher tidal ranges the beach tends to widen (Masselink, 1993). Tides also may alter sediment transport (Short, 1999).

Beaches can be classified into three types based on the relative tidal range parameter (RTR)[1], which measure the relative importance of tides and waves in influencing the beach morphology: low values (RTR<3) indicate wave-dominated beaches; values in the range 3 to 10 indicate tide-modified beaches; and RTR >10 indicates tide-dominated beaches. These three broad categories can be subdivided into a range of beach states considering also the role of wave period and sediment size (all these parameters included in Dean's index[2]) (Fig. 2; Short and Jackson, 2013). When waves dominate morphology, as occurs in areas of micro-tides (i.e. tidal range < 2m), the morphology of the location and the spatial extent of surf and swash zones are relatively fixed. Depending of the wave height and grain size, beaches can be classified into three main types: (i) reflective, which occurs when conditions are calm (i.e. wave height < 0.5m) and/or the sediment is coarse (approx. ≥ 400μm). There is no true surf zone and waves break directly on the beach face. Moreover, these beaches have steep slopes and the swash tends to be turbulent; (ii) dissipative, which tends to high waves (> 2.5 m) and fine sand (approx. ≤ 200μm). Waves are largely dissipated in a broad surf zone before reaching the intertidal sand, resulting in a gentle beach slope and non-turbulent swash (Masselink and Short, 1993; Short, 1999). Between these two extremes, four intermediate states are recognized (see Short, 1999 for more details). As tidal range increase (e.g. mixed or tide-modified beaches), these zones (surf and swash) are translated shoreward and seaward, resulting in a blending of the three distinct processes and to some extent the three associated morphologies (Fig. 2). Consequently, the equilibrium conditions on the intertidal profile are defined by a mixture of different hydrodynamic processes that depend on the specific location as well as wave, tide and sediment characteristics (Masselink and Short, 1993; Short, 1999 for more details).

[1] RTR = TR/H_b, where TR is the mean spring tidal range and H_b is the breaker-wave height.

[2] Dean index: $\Omega = H_b / ws \times T$, a function of wave-breaker height (H_b), sedimentation velocity (ws) and wave-breaker period (T).

- *Faunal diversity in sandy beaches*

Despite their initial barren and sterile appearance, sandy beaches and dunes contain a unique faunal biodiversity that encompasses a wide range of animal taxa, many of which live nowhere else (Schlacher et al., 2014). Beach fauna includes resident invertebrate species, many of which are direct developers and hence have limited dispersal ability. There are also fish and invertebrates (e.g. insects, arachnids) species, which use beaches and surf zones for some portion of their life cycle. Moreover, wildlife species (e.g. birds, reptiles, marine mammals) depend on beaches and dunes for roosting, nesting, chick rearing, feeding on wave-vast carrion or as foraging areas during wintering and migrations (Schlacher et al., 2014). However, overall, only a few species present abundant populations in sandy beaches, especially among macroinvertebrates. The major macroinvertebrate taxa on exposed sandy beaches are arthropods (crustaceans, insects and, spiders), molluscs (clams and snails) and annelids (polychaetes and oligochaetes) (McLachlan and Brown, 2006). These macroinvertebrates can reach high abundance (ca. 100,000 ind. m^{-1}) and biomass (> 1,000 g m^{-1}), particularly in dissipative to intermediate beach types in temperate zones (Defeo et al., 2009). However, the diversity is relatively low in these systems compared with other littoral systems, causing a high sensitivity to environmental changes (McLachlan and Brown, 2006). Most beach species cannot be found in any other environment and they display a range of unique adaptations to this highly dynamic and unstable environment, including mobility and burrowing abilities, rhythmicity in their behaviour, complex orientation mechanisms and plasticity (e.g. Brown, 1996; Scapini, 1997; Dugan et al., 2000; Scapini, 2006; Lastra et al., 2010; Scapini, 2014).

Until now, it was thought that the structure of assemblages (i.e. abundance, species richness, and diversity) in sandy beaches within a one geographical region is the result of the independent responses of individual species to the physical environment whereas biological interactions are minimal (Jaramillo and McLachlan, 1993; McLachlan et al., 1993; Jaramillo et al., 2001; Defeo and McLachlan, 2005; McLachlan and Dorvlo, 2005; Defeo and McLachlan, 2011). There is a general trend, for instance, of increasing species richness with decreasing grain size and beach face slope, increasing tidal range and intertidal width and/or decreasing harsh swash climate (e.g. Jaramillo and McLachlan, 1993; Brazeiro, 1999; McLachlan and Dorvlo, 2005).

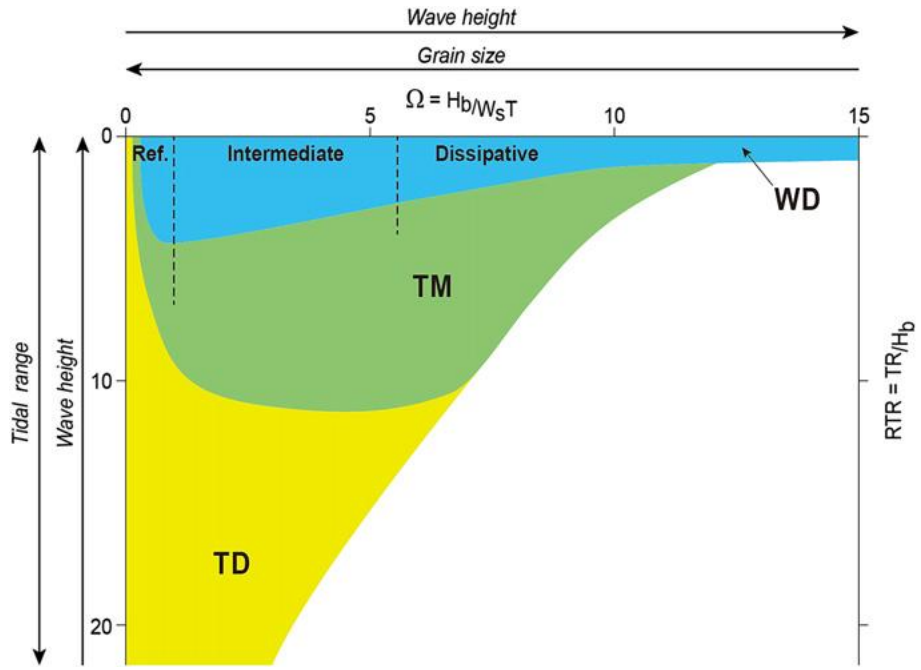

Figure 2.Dean´s parameter (Ω) versus relative tide range (RTR) showing the general domain of reflective (ref), intermediate and dissipative beaches through the wave-dominated (WD), tide-modified (TM) and tide-dominated (TD) beach types (Modified from Short and Jackson, 2013).

Gradually, however, a greater number of studies are showing the relevance of biotic interactions and environmental factors (e.g. moisture, temperature, pH, food supply, etc.) to explain the structure of macroinvertebrate assemblages on exposed beaches (Dugan et al., 2004; Lastra et al., 2006; Rodil et al., 2007; Ortega Cisnero et al., 2011; Rodil et al., 2012). Within a single beach, the spatial distribution of macroinvertebrates presents several peculiar features such as patchiness, complex zonation patterns related to the tidal gradient, and fluctuations due to tidal and other migrations (Defeo and McLachlan, 2005; McLachlan and Brown, 2006; Scapini, 2014). Regarding the zonation of macroinvertebrates, several attempts have been made to find similar universal zonation patterns on sandy beaches than those found on rocky shores (e.g. Stephenson and Stephenson, 1949; Southward, 1958; Benedetti-Cecchi, 2001). Recent studies support the existence of three biological zones on exposed sandy beaches (Defeo and McLachlan, 2005; Schlacher and Thompson, 2013): (1) supralittoral zone, situated at and above the drift line and typically inhabited by talitrid amphipods, oniscid isopods or ocypodid crabs in tropical and subtropical beaches. The diversity and abundance of species in this zone is increased in sandy beaches subsidized by marine organic debris (e.g. Dugan et al., 2003; Jaramillo et al., 2006; Gonçalves and Marques, 2011); (2)

midlittoral zone, between the drift line to around the effluent line with a more diverse mixture of true intertidal species (e.g. cirolanid isopods, several families of amphipods, and spionid polychaetes); (3) sublittoral zone, extending from near the effluent line into the swash and characterised by the most species-rich communities including crabs, mysids, clams, and several families of amphipods and polychaetes. In contrast to rocky shores, exposed sandy beaches are extremely dynamic and unstable habitats inhabited by highly mobile species with plasticity in their behaviour, which can result in variable distributions. Moreover, beach species may vary the range of distribution across the intertidal daily and seasonally (Scapini, 1997; Gambineri et al., 2008; Fanini et al., 2012). These properties of beach habitats and organisms make spatial structure less distinct and more variable in space and time than on rocky shores (Brazeiro and Defeo, 1996; Schlacher and Thompson, 2013; Veiga et al., 2014).

- *Beach as ecosystem*

Sandy beaches contain structurally heterogeneous habitats that support rich and diverse biological communities, and these also constitute functionally dynamic ecosystems (Defeo et al., 2009; Schlacher et al., 2008; Schlacher et al., 2014). Surf zones, beaches and coastal dunes form a single functional unit, exchanging organisms, sand, organic matter, and nutrients. Particularly, the exchanges of organic matter (e.g. phytoplankton, dune plants, and marine organic debris) through the beach constitute one of the most important processes in maintaining the energy flow between the terrestrial and marine systems (McLachlan and Brown, 2006; Mellbrand et al., 2011). Moreover, organic materials are exploited by a wide range of consumers across several trophic levels from macroinvertebrate scavengers, meiofauna, and bacteria to higher terrestrial predators such as birds, lizards, and mammals which interacted in a complex food web (Dugan et al., 2000; Dugan et al., 2003; Catenazzi and Donnelly, 2007; Lastra et al., 2008; Spiller et al., 2010; Colombini et al., 2011a).

- **Supralittoral ecology**

The upper zone or supralittoral is the zone above the MHHW (mean higher high water) influenced by spray and extreme high tides (Fig. 3). As interface between land and sea, this zone is a unique ecotone but little studied by marine and terrestrial ecologists (Attrill et al., 1999). This zone possesses some properties common to both systems and is a dynamic zone of great importance in energy exchange and nutrient flux in the

nearshore ecosystem (Polis and Hurd, 1996; Zimmer et al., 2002; Mellbrand et al., 2011). Supralittoral ecology is driven by terrestrial as well as marine processes including marine wrack deposition, terrestrial litter inputs, sediment deposition from bluff erosion or dunes, recycling and decomposition of organic detritus, and export of organisms to the nearshore food web (Fig. 4). The physical factors affecting the ecology of this zone include: exposure, tidal current and height, and sediment grain size (McLachlan and Brown, 2006). This environment is also constantly drying out and, therefore, desiccation and temperature are the main stress factors for the fauna.

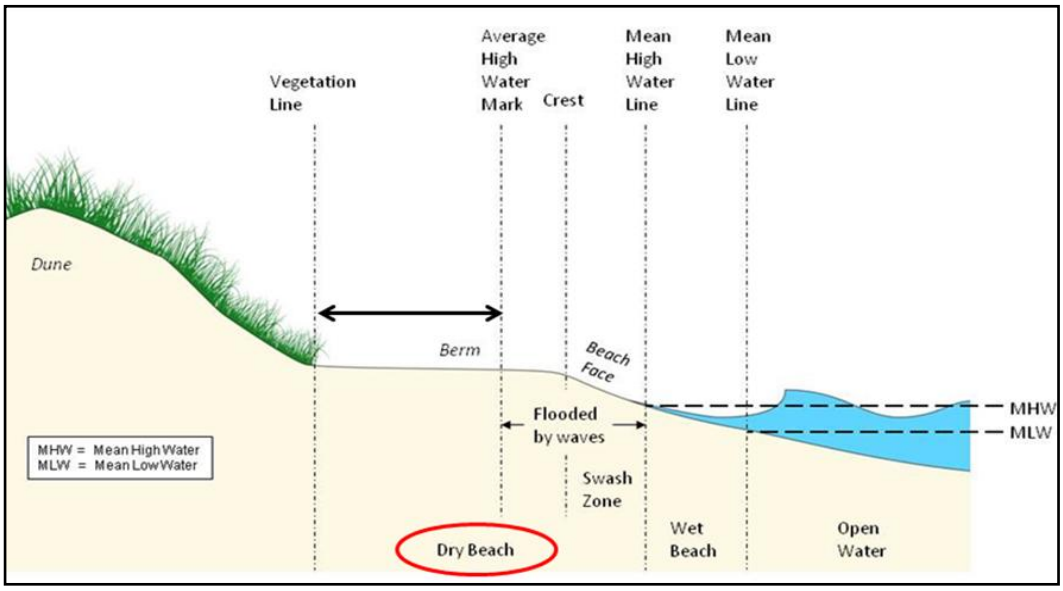

Figure 3.Tidal zonation along an exposed beach (Titus, J., 2011). *Wet beach* is defined as the land between the mean low water line and the mean high water line. *Dry beach* is defined as the land between the dune vegetation line and the mean high water line. During an average high tide, several waves generally run up over the crest, leaving a water mark on the sand and sometimes debris such as seaweed at the average high water mark. The zone above the MHHW is called upper zone or supralittoral zone.

- *Beach wrack deposits*

Beach wrack, also called "beach cast" or "drift" (i.e. the agglomeration of organic debris deposited on the beach surface by an ebbing tide), is an important supralittoral component on sandy shores (Colombini and Chelazzi, 2003). These organic materials come from adjacent coastal ecosystems (rocky intertidal, rocky shores, seagrass meadows, mangroves) associated with offshore dynamics and physical factors such as currents, prevailing winds, waves and tides, which transport organic materials and leave

accumulations of them along shores during the ebbing tide to form driftlines (e.g. Ochieng and Erftemeijer, 1999; Orr et al., 2005).

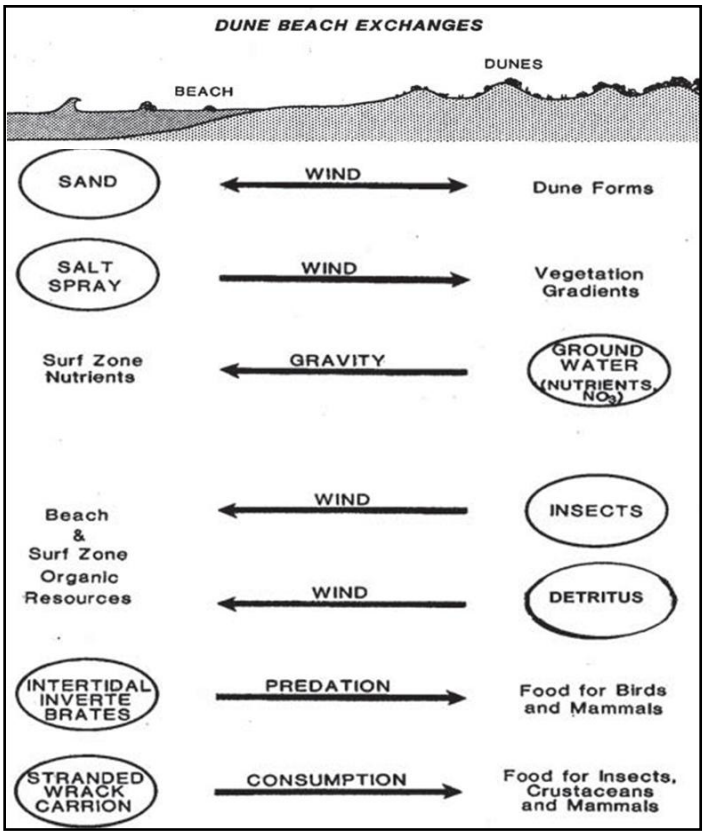

Figure 4.Exchanges of materials between the dune and the intertidal on sandy beaches (McLachlan and Brown, 2006).

In many temperate regions, driftlines are composed mainly of seagrasses, kelps and marine macroalgae, but mangrove propagules and carrion represent other major organic components of beach cast (Fig. 5). Mangrove propagules are common in tropical and subtropical areas, while the carrion becomes important on beaches with very low allochthonous inputs (Colombini and Chelazzi, 2003). The standing crop on any beach depends on the production in the donor ecosystems and the physical elements involved in their transport (Stenton-Dozey and Griffiths, 1983; Orr et al., 2005; Mateo, 2010). The spatial and temporal variability in wrack supply and composition are commonly associated with random events. However, a recent study reported that the variability in wrack biomass and composition on sandy beaches can be explained through interactions between wave exposure, coastal topography and seasonality (Barreiro et al., 2011).

The deposition pattern of wrack debris is highly influenced by the physical beach environment (e.g. rate of exposure, beach slope, wave height, type of substratum,

and swash environment) and by the composition and buoyancy of the drifting wrack (Ochieng and Erftemeijer, 1999; Orr et al., 2005; Barreiro et al., 2011; Duong and Fairweather, 2011). These deposits commonly show a patchy distribution throughout the entire intertidal range, creating a mosaic of bare and wrack-occupied areas (Colombini et al., 2000; Rossi and Underwood, 2002; Jaramillo et al., 2006). The spatial distribution of the wrack debris along the beach profile depends on where the wrack strands during the ebbing period. In the upper zone, wrack debris lies beyond the reach of the wave action and can be present in the supralittoral zone for a long period in comparison to wrack debris deposited in the midlittoral zone, where these are influenced by the physical forces of waves, tides and sediment movement during the entire period of stranding (Ochieng and Erftemeijer, 1999; Orr et al., 2005). On the upper shores, wrack can be deposited along one or more drift lines, usually at the spring high-water line and in bands or in a band[3] down to the level of the most recent high tide (Marsden, 1991; Ochieng and Erftemeijer, 1999; Colombini et al., 2000).

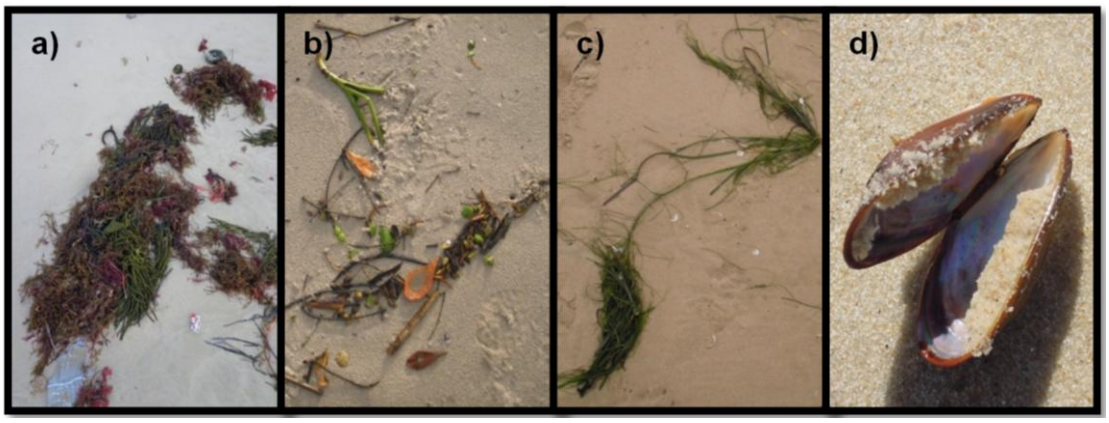

Figure 5.Wrack composition a) macroalgae, b) mangrove propagules, c) seagrass, and d) carrion.

Once stranded on the upper shores, wrack debris dehydrates and ages, this influencing the microclimatic conditions (i.e. temperature and moisture) and nutritional composition of the wrack deposits (Olabarria et al., 2007; Rodil et al., 2008; MacMillan and Quijón, 2012). Therefore, these habitat features (i.e. biochemical composition of organic matter and microclimatic conditions) could change spatially, in relation to the tidal height in which wrack is deposited at the supralittoral zones (i.e. bands), and temporally as the organic material ages and undergo the physical dynamics of the beach

[3] Band is defined as the line parallel to the tide line covered of wrack.

environment (wind, sand covering, solar exposure, dehydration, etc.) on wrack debris. However, these processes are complex and depend on multiple factors such as the amount and composition of wrack deposits on the upper shores (Jedrzejczak, 2002a; Rodil et al., 2008).

- *Supralittoral macroinvertebrates*

Traditionally, studies on community structure and zonation patterns have focused on intertidal macrofauna in sandy beaches worldwide (e.g. Defeo et al., 1992; Dexter, 1992; Jaramillo and McLachlan, 1993; Souza and Gianuca, 1995; Brazeiro and Defeo, 1996; McLachlan et al., 1996; Veloso et al., 2003; Rodil et al., 2006). However, little attention has been given to terrestrial arthropods (i.e. dipterans, coleopterans, isopods, amphipods) inhabiting the supralittoral zone, although it has recently been demonstrated that they have an important place in the structure and composition of the whole macrofauna community (de la Huz and Lastra, 2008; Gonçalves et al., 2009; Gonçalves and Marques, 2011) as well as in the coastal food web (Dugan et al., 2003; Dugan and Hubbard, 2010; Spiller et al., 2010; Laffety et al., 2013).

The supralittoral fauna associated with wrack is typically dominated by insects in terms of species (with beetles and flies most common) but crustaceans, especially talitrid amphipods, are numerically dominant (Inglis, 1989; Jedrzejczak, 2002b; Lastra et al., 2008; MacMillan and Quijón, 2012). Wrack-associated fauna play an important ecological role in sandy-shore functions, because they occupy a key position in the centre of food chains (McLachlan and Brown, 2006). Several species of scavengers (i.e. primary consumers), such as crustaceans and insects, are known to feed upon beach wrack, having an important impact on organic-detritus processing (see for instance Lastra et al., 2008). In turn, macroinvertebrates serve as prey for secondary consumers, such as carnivorous beetles and spiders (Ince et al., 2007; Colombini et al., 2011a) and for top predators such as shorebirds, lizards, rodents, etc. (Anderson and Polis, 1998; Hubbard and Dugan, 2003; Catenazzi and Donnelly, 2007; Spiller et al., 2010).

It is known that intertidal fauna is controlled by the morphodynamic state of the beach and the variations in the physical environment. However, the upper shore macroinvertebrates are not clearly affected by physical processes associated with the beach morphodynamic state and, therefore their distributional patterns are explained by other factors such as wrack availability (de la Huz and Lastra, 2008). On sandy shores with high amounts of wrack, algal wrack can create a new habitat with different

microclimatic characteristics than the surrounding areas (Colombini and Chelazzi, 2003) and provide organic matter to poorly productive supralittoral zone (McLachlan and Brown, 2006). This process increases the spatial heterogeneity and, in turn, the range of microhabitats available for macroinvertebrates. As shown by previous studies, the abundance and the number of invertebrate species is higher in wrack patches than in bare sediments on the upper shores (Dugan et al., 2003; Jaramillo et al., 2006; Ince et al., 2007; Rodil et al., 2008; MacMillan and Quijón, 2012). The reliance of macroinvertebrates on wrack is generally understood as a response to food resource or shelter from predation and against the harsh environmental conditions (i.e. temperature and dryness) of supralittoral zones (Dugan et al., 2003; Jaramillo et al., 2006; Ince et al., 2007; Olabarria et al., 2007; Lastra et al., 2008). However, the abiotic factors (i.e. microclimatic conditions, food availability, nutritional composition, etc.) structuring supralittoral communities as the result of the establishment of algal wrack deposits are poorly understood. Relationships between the habitat features of wrack debris and the density of arthopod species provide the opportunity to advance in understanding the factors structuring the diversity and composition of supralittoral assemblages.

The interaction between wrack deposits and macroinvertebrates is considered a dynamic process which is highly spatially and temporally variable (Colombini and Chelazzi, 2003). Often, wrack deposits are accumulated in bands parallel to tidal lines on the upper shores. The position on the supralittoral zone determines the relative age (i.e. dehydration and decomposition degree) of wrack deposits, which influence the spatial distribution of macroinvertebrates, depending on the preference for specific microhabitats and/or food sources, which differ according to the species (e.g. Marsden, 1991; Jaramillo et al., 2006; Rodil et al., 2008; MacMillan and Quijón, 2012). The distributional pattern of wrack-associated fauna in relation to the relative age of wrack debris has been studied locally and only using algal wrack debris. Therefore, the potential ecological role of the composition and relative age of wrack deposits on the structure of supralittoral assemblages remains unknown.

The structure and composition of macroinvertebrate assemblages associated with wrack debris can also vary temporally as the result of complex colonization processes in a patch of new habitat (Inglis, 1989; Olabarria et al., 2007; Dufour et al., 2012). Species-specific strategies for exploiting wrack (as refuges and/or as a feeding site) and the colonizing and competitive abilities of different taxa may lead to temporal changes in assemblages associated with wrack debris (Griffiths and Stenton-Dozey, 1981; Inglis,

1989; Marsden, 1991; Colombini et al., 2000; Olabarria et al., 2007; Rodil et al., 2008; Dufour et al., 2012). Previous studies have demonstrated that the colonization patterns in artificial algal wrack patches result of a directional replacement of species, i.e. from domination by "early" species to domination by "late" species. In this way, most of studies have reported talitrid amphipods as well as tylid and oniscoid isopods as primary colonizers of wrack patches, while different insect species, mainly dipterans and coleopterans, tend to colonize algal patches in late stages (e.g. Griffiths and Stenton-Dozey, 1981; Behbehani and Croker, 1982; Inglis, 1989; Colombini et al., 2000; Jedrzejczak, 2002b; Olabarria et al., 2007). However, natural wrack patches are highly variable, because of the specific habitat attributes of wrack accumulations change temporally as the organic material undergoes the dynamics of the beach environment (i.e. stranded and ageing or re-deposited and re-exposed in successive tides). Therefore, natural wrack accumulations are composed of wrack patches with different stages of ageing (i.e. from new and fresh materials to dry and highly decomposed materials) and, consequently, with different habitat attributes, which can broaden the range of habitats available for supralittoral arthropods. After a natural disturbance (i.e. the stranding of wrack debris) a directional change in assemblages could not be expected (Platt and Connell, 2003). Monitoring colonizer species in stranded wrack debris could provide basic information to understand the temporal changes in composition and structure of macroinvertebrate assemblages associated with natural wrack debris.

- **Wrack removal as disturbance for strandline macroinvertebrates**

Ocean beaches are considered a pivotal economic asset, attracting more tourists and recreational users than most other coastal ecosystems (Defeo et al., 2009). Burgeoning coastal populations, coupled with more leisure time and improved mobility, have escalated the intensity and spatial ambit of beach recreation over recent decades (Schlacher et al., 2007; Defeo et al., 2009). In this scenario, beach management traditionally tries to achieve a high aesthetic quality of the beach, i.e. beaches are only considered as landscapes of intense human use at the expense of the ecological quality of the beach environment (McLachlan et al., 2013). Activities to improve the perception of the beach-goers are central in the management plans (Davenport and Davenport, 2006; McLachlan et al., 2013). Tourists often interpret stranded natural debris as poor water and low beach quality, especially if the materials start to decompose. Moreover,

bathing water quality is perceived as one of the key issues by beach users (Williams and Micallef, 2009). Therefore, wrack debris is subject to recreational beach management, being mechanically or manually removed from sandy beaches worldwide (Kirkman and Kendrick, 1997; Micallef and Williams, 2002; Dugan et al., 2003; Fairweather and Henry, 2003; Gilburn, 2012). This management activity is concentrated on the upper beach, where stranded wrack remains for several days, weeks or even months (Colombini and Chelazzi, 2003; Orr et al., 2005). Nevertheless, previous studies have indicated that removal of wrack may be ecologically damaging by disrupting pathways of decomposition and nutrient exchange between marine and terrestrial ecosystems as well as by altering the composition of upper-shore invertebrate communities and prey availability to higher trophic levels, such as shorebirds, lizards, and rodents (e.g. Llewellyn and Shackley, 1996; Kirkman and Kendrick, 1997; Dugan et al., 2003; Fairweather and Henry, 2003; Martin et al., 2006; Spiller et al., 2010; Dugan et al. 2011; Barreiro et al., 2013; Gilburn, 2012; Lafferty et al., 2013).

Supralittoral arthropods, including those associated with strandlines, are considered a suitable indicator of changes and impact on beach ecosystems, since they respond rapidly to any change to the local environment (Kremen et al., 1993; Colombini et al., 2003; Gerlach et al., 2013). Their small size makes them sensitive to local conditions, while their mobility enables them to move in response to changing conditions. In turn, short generation times result in rapid numerical responses, and variability in ecological characteristics give a wide range of specific environmental-response taxa (Gerlach et al., 2013). On sandy beaches, studies on human impact (e.g. trampling, recreational activities, beach cleaning, etc.) on the supralittoral zone have targeted specific populations within the arthropod fauna, most commonly talitrid amphipods (Jaramillo et al., 1996, Fanini et al., 2005, Veloso et al., 2006; Veloso et al., 2009; Vieira et al., 2012). In particular, the amphipod *Talitrus saltator* has been used as a tool to assess impact related to recreational activities on Mediterranean, Baltic, and Atlantic sandy beaches (Welaswski et al., 2000; Nardi et al., 2003; Ugolini et al., 2008; Veloso et al., 2008; Fanini et al., 2009; Scapini and Ottaviano, 2010; Bessa et al., 2013). *T. saltator* is an opportunistic species characterized by a short life span, abundant population, and wide geographical distribution, making it suitable for environmental monitoring (Marques et al., 2003; Scapini, 2006). In addition, the role of talitrid amphipods is crucial for the sandy-beach ecosystem, as they are important links in the food chain between macrophyte supply and higher trophic levels, such as avian

consumers (Dugan et al., 2003; McLachlan and Brown, 2006). Furthermore, some studies have used beetles or spiders as bioindicators of human disturbances in sandy beaches (e.g. Colombini et al., 2003; Comor et al., 2008; Schierding et al., 2011; Irlmer, 2012). However, few studies have undertaken community-level analyses, although arthropod fauna could be also a suitable bioindicator of beach disturbances, since the variability in ecological characteristics give a wide range of specific environmental response taxa (Kremen et al., 1993; Colombini et al., 2003; Gerlach et al., 2013).

Previous studies have reported that macrofaunal communities intrinsically associated to wrack are disrupted, i.e. reduced in species abundance and richness, as a result of mechanical beach cleaning (Llewellyn and Shackley, 1996; Dugan et al., 2003; Gilburn, 2012). However, these studies used "compare and contrast" design in which the putative effects of the wrack removal on macroinvertebrate assemblages can be confounded with those associated with mechanical cleaning (i.e. removal of sand, crushing of organisms, redistribution of animals, deeper burial, etc.) and other potential anthropogenic impact on urban beaches, such as trampling, recreational activities or habitat alteration (e.g. artificial structures), which may disturb macroinvertebrates (e.g. Fanini et al., 2005; Colombini et al., 2011b; Schlacher and Thompson, 2012; Bessa et al., 2014). On the contrary, manipulative experiments are a good way to evaluate the direct effect of a disturbance (Glasby and Underwood, 1996). Because of the high spatial and temporal variability of beach populations (McLachlan and Brown, 2006; Schlacher et al., 2008), there is considerable interaction between space and time in the data from any sampling design. In this way, M-BACI (multiple-before-and-after-control-impact) (Downes et al., 2004; Underwood, 1994) allows an appropriate spatial and temporal replication (i.e. multiple locations and several times of samplings) to analyse the response of natural communities and/or populations to environmental disturbances in sandy beaches. However, M-BACI is not a common methodology to evaluate the effect of disturbances on sandy beaches. Therefore, a manipulative experiment using the M-BACI design could be an informative way to assess the direct effects of the wrack removal on strandline-associated fauna. Given that wrack-associated fauna are characterized by highly mobile species that can colonise impacted areas after the disturbance, may be useful indicators of the process of change, as their return will indicate the ongoing recovery. Therefore, supralittoral assemblages (i.e. the whole of the community structure) and specific populations, such as talitrid amphipods, can be used as a bioindicator of wrack removal from the upper beaches.

➢ Aims and thesis structure

Because sandy beaches have very low *in situ* primary production, wrack debris deposited on the beach surface provide the main source of food and/or refuge to macrofaunal communities, mainly to supralittoral arthropods (such as talitrid amphipods, oniscoid isopods, coleopterans, arachnids, etc.). On the upper beach, wrack debris is accumulated along strandlines, where forming a highly dynamic environment. Therefore, the spatial and temporal variability in wrack distribution and its habitat features (i.e. moisture, temperature, ageing, etc.) may influence the composition and structure of supralittoral assemblages. Moreover, the temporal suppression of wrack supply due to the removal of wrack debris can alter the structure and composition of associated assemblages, but its direct effect on these assemblages remains poorly understood. Therefore, for this thesis, observational and field experimental studies were performed to evaluate the spatio-temporal variation of the supralittoral arthropods inhabiting strandlines and their biological responses to human disturbances such as the wrack removal, which, in turn, is relevant to the management of this key resource (i.e. wrack debris) on sandy beaches.

The general aim of this thesis was to increase our understanding of the spatio-temporal variation in the distribution and utilization of wrack debris by supralittoral arthropods. Particularly, this thesis attempts to detect patterns in the spatial and temporal distribution of wrack-associated fauna, with attention to the factors that could explain these distributional patterns, as well as to investigate response patterns of these assemblages to the removal of wrack debris in Atlantic upper shores.

For this purpose, this work is structured in five parts: the first part provides the general introduction, the second and third parts concern the research chapters, and the fourth and fifth parts present the general discussion and the main conclusions of this work. The research chapters included in the second and third parts of this thesis are detailed below.

- *Part II: The role of wrack debris for supralittoral arthropods: spatial and temporal patterns*

On the upper beach, wrack debris are deposited at different tidal levels and are locally redistributed through wind, creating a mosaic of bare and wrack-occupied areas which influence on the distribution of invertebrate assemblages. Moreover, this natural

disturbance (i.e. the stranding of wrack debris) creates an opportunity for new individuals to become established. This could trigger colonization patterns, and, consequently, determine the temporal variation in the composition of invertebrate assemblages.

This part is devoted to analysing spatial and temporal patterns of supralittoral assemblages in relation to the wrack distribution and its habitat features on the upper shores. **Chapter 1** examines the influence of the position (at different tidal levels) and the relative age (i.e. the relative state of decomposition and degree of dehydration) of upper wrack deposits on the composition and structure of macroinvertebrate assemblages. The standing crop and the associated macroinvertebrates are evaluated on six sandy beaches located at Brazilian and Spanish Atlantic coasts to analyse whether, disregarding species differences, there are similar distributional patterns of supralittoral arthropods as a response of the relative age of wrack deposits. The effect of the spatial distribution (i.e. bands) of wrack debris on the structure of supralittoral assemblages is discussed. The results of this chapter have been published in *Estuarine, Coastal and Shelf Science*.

This pioneer study on the role of wrack distribution and its relative ages on the structure of supralittoral assemblages is complemented with a local study (i.e. south-western Spanish Atlantic coast) about the spatio-temporal changes of the habitat features (i.e. microclimatic conditions, food availability and nutritional content) of upper-shore wrack deposits and their relationship with the faunal distribution in the **Chapter 2**. Particularly, the habitat features were measured in wrack patches and bare sand at the upper and lower tidal levels on the upper beach and its relationships with macroinvertebrate assemblages and the density of the dominate species were also analysed for two contrasting seasons (i.e. winter and summer). The distributional pattern of macroinvertebrates in relation to the spatio-temporal changes of habitat features on the upper beach is discussed. Moreover, the reliance of arthropods on wrack debris as shelter and/or feeding site is also discussed. The results and conclusions obtained in this chapter were published in *Hydrobiologia*.

Finally, **Chapter 3** is focused on the temporal changes in macroinvertebrate assemblages during the colonization of natural strandlines on the upper beach. In particular, the presence of stranded wrack was manipulated, removing or not removing wrack debris, and then wrack-associated fauna (i.e. abundance, richness, and coloniser species) was monitored after the stranding of new wrack debris in a short-term period

(47 days). This field experiment was performed on Atlantic sandy upper shores of the south-western Spain and southern Brazil in order to describe colonization patterns in response to the stranding of natural wrack debris. Temporal changes in assemblages and the species responsible of these changes during the colonization of strandlines was analysed. The patterns of colonization in both studied regions were further discussed. The results and conclusions of this chapter are *in preparation* to be submitted in *Marine Ecology*.

- *Part III: Wrack removal as a source of disturbance for supralittoral macroinvertebrates*

Wrack debris provides both a physical structure (which can be used as shelter and breeding sites) and a source of food to macrofaunal communities, mainly to terrestrial invertebrates such as talitrid amphipods, dipterans and coleopterans which dominate the upper beach. Since many of these organisms act as linkage between organic inputs and higher trophic consumers, the availability of wrack to support their abundance and biomass is a key factor to maintain the abundance and the diversity of marine and terrestrial ecosystems, as well as the energy flows between the two ecosystems. Nevertheless, wrack debris is commonly removed from sandy beaches worldwide, and studies concerning its effect on strandline macrofaunal species are scarce.

An experimental design (following the M-BACI) was performed to assess the short-term (days) effects of wrack removal on supralittoral assemblages. For this, the biological responses were compared before and after to remove all organic debris detached at the upper shores. This objective was dealt with in two chapters. **Chapter 4** focuses on analysing the potential effect of this disturbance on the whole assemblage (i.e. density, species richness, and community structure). This experiment was perfomed on sandy beaches of two different regions (Brazil and Spain) to evaluate whether, disregarding species differences, the reduction of wrack availability involves similar response patterns in the structure of the communities associated with wrack debris. On the other hand, in the **Chapter 5** evaluates the effect of wrack removal using the bioindicator *Talitrus saltator* on two European Atlantic sandy beaches. The effect of the reduction of stranded wrack biomass was analysed regarding the total density and the density of adults and juveniles individuals of the *T. saltator* associated with stranded wrack in the supralittoral zone. The ability of the supralittoral macroinvertebrates to recover after a disturbance at the strandlines is discussed, focusing on results of talitrid

amphipods, and the implications of the results of these experiments for the management of wrack debris. Moreover, the M-BACI design is presented as a robust methodology to evaluate enviromental disturbances in sandy beaches. The results and conclusion of Chapter 4 are *in preparation* to submit *in Journal of Experimental Marine Biology and Ecology*, while those of the Chapter 5 are submitted in *Estuaries and Coasts.*

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PART II: CHAPTER 1

THE ROLE OF WRACK DEPOSITS FOR SUPRALITTORAL ARTHROPODS: AN EXAMPLE USING ATLANTIC SANDY BEACHES OF BRAZIL AND SPAIN

The role of wrack deposits for supralittoral arthropods: an example using Atlantic sandy beaches of Brazil and Spain

ABSTRACT

Wrack deposits, a common feature on beaches worldwide, significantly contribute to the shaping of supralittoral arthropod communities. The composition and relative age of upper-shore deposits influence the structure and taxonomic composition of invertebrate assemblages. Moreover, these influences may vary geographically, depending on the locally prevailing climatic and hydrodynamic conditions. The amount and composition of wrack deposits as well as community attributes (total density, species richness and diversity) were determined on sandy beaches located in three distinct geographical regions: South (Paraná) and Southeast (Rio de Janeiro) of Brazil and Southwest of Spain. These parameters were compared between upper and lower wrack bands on each beach and between beaches in each region. Wrack deposits were composed of mangrove propagules in Paraná region, by macrophytes, dead invertebrates and macroalgae in Rio de Janeiro region and by seagrass and macroalgae in Southwest of Spain region. In all regions, the total amount of stranded wrack differed between beaches, but the amount accumulated between bands (i.e upper and lower band) was similar between beaches. Wrack bands shaped density of common taxa (Talitridae, Tenebrionidae, and Staphylinidae), with consequences in communities structures. This result could be due to their preference for specific microhabitats and food sources, which might differ according to the relative age of the wrack deposits. The results suggests that, independent of wrack composition, the distribution of wrack deposits in bands and their relative ages seems to play a role on the structure of supralittoral arthropod assemblages.

Key words: wrack, driftlines, supralittoral arthropods, ageing, sandy beaches, Atlantic coast, south of Brazil, southwest of Spain.

INTRODUCTION

Stranding organic allochthonous materials is a common feature on sandy beaches around the world. These systems are generally characterized by the action of strong hydrodynamic forces that create unconsolidated sands devoid of large primary producers (McLachlan, 1981; Griffiths et al., 1983). Beach food webs in these environments are supported primarily by allochthonous resources. Organic materials come from adjacent coastal ecosystems (rocky intertidal, rocky shores, seagrass meadows, mangroves) associated with offshore dynamics and physical factors such as currents, prevailing winds, waves and tides, which transport organic materials and leave accumulation of them along shores to form wrack deposits (e.g. Ochieng and Erftemeijer, 1999; Orr et al., 2005). In many temperate regions, these wrack deposits are composed mainly of marine macrophytes and macroalgae, but mangrove propagules and carrion represent other major organic components of beach cast. The former are common in tropical areas while the latter become important on beaches with very low allochthonous inputs (Colombini and Chelazzi, 2003).

The amount and spatial distribution of allochthonous materials at a given beach may vary according to: the production of the adjacent habitats; the physical environment of beaches (e.g. rate of exposure, beach slope, wave height, type of substratum and swash environment) and the composition and buoyancy of the drifting wrack (Ochieng and Erftemeijer, 1999; Orr et al., 2005; Barreiro et al., 2011; Duong and Fairweather, 2011). Over the entire of a beach, wracks can be distributed into patches from the extremely high water of spring tide to mean tidal levels or can be deposited along one or more drift lines, usually at high water spring line and in bands or in a band down to the level of the most recent high tide (Marsden, 1991, Ochieng and Erftemeijer, 1999, Colombini et al., 2000). Such distribution patterns affects the abundance and distribution of invertebrate assemblages, particularly supralittoral invertebrates (e.g. Stenton-Dozey and Griffiths, 1983; Jaramillo et al., 2006; Olabarria et al., 2007). Several authors reported higher abundances and species richness of invertebrates in wrack patches than in bare sediments (Dugan et al., 2003; Jaramillo et al., 2006; Ince et al., 2007; Rodil et al., 2008; McMillan and Quijón, 2012). In addition, the position of wrack deposits over the beach surface determines the beach inhabitants that can colonize them (Colombini et al., 2009). Wrack deposits in the middle and lower-shore are more likely to be colonised by marine taxa, whereas upper-shore deposits are likely

to be dominated by terrestrial taxa, mainly insects and their larvae (Egglishaw, 1965). Furthermore, upper-shore deposits are subject to dehydration, ageing and sand covering, encouraging their decomposition and remineralization (Griffiths and Stenton-Dozey, 1981; Inglis, 1989; Jedrzejczak, 2002a). These processes are complex and depend on the amount and composition of wrack (Jędrzejczak, 2002a; Rossi and Underwood, 2002).

Different types of wrack such as macroalgae and propagules may vary in their physical characteristics, which could determine their decomposition rates, nutritional values and also microclimatic conditions (i.e. temperature and humidity) (Rodil et al., 2008). Therefore, the composition and the age of wrack might influence the structure and taxonomic composition of invertebrate assemblages, depending on the preference for specific microhabitat and food sources that differ according to species (Valiela and Rietsma, 1995; Colombini et al., 2000; Pennings et al., 2000). Talitrid amphipods as well as tylid and oniscoid isopods are considered primary colonizers of newly deposited wrack, while different insect species, mainly dipterans and coleopterans, colonize the deposits when these dry out (e.g. Griffiths and Stenton-Dozey, 1981; Behbehani and Croker, 1982; Inglis, 1989; Colombini et al., 2000). In addition to their use as refuges, wrack deposits represent the main food resource for supralittoral invertebrates. The distribution pattern of wrack-associated fauna is related to feeding preference of individual species for a type of resource as a food (Colombini and Chelazzi, 2003). Because many of these organisms form the base of coastal food chains, their abundance and the availability of food resource to support their biomass are important factors in the abundance and diversity of beach ecosystems (Dugan et al., 2003; Ince et al., 2007).

Large amounts of wrack (mostly macroalgae) have been quantified worldwide (Stenton-Dozey and Griffiths, 1983; Polis et al., 1997; Ochieng and Erftemeijer, 1999, Dugan et al. 2003; Orr et al. 2005; Barreiro et al., 2011) with important effects for the macrofaunal community (Colombini and Chelazzi, 2003). However, few studies have evaluated wrack biomass of different types of allochthonous materials such as macroalgae, seagrass and mangrove propagules and their associated invertebrate assemblages. Apart from the amount and composition of stranded wrack, the position and the relative age of upper wrack deposits influence the composition and structure of wrack-associated fauna (Colombini et al., 2000; Jaramillo et al., 2006; Rodil et al., 2008). Moreover, most of the studies on this topic have been conducted on a local scale, so that it remains unknown whether the ecological role of the composition and relative

age of wrack deposits on the supralittoral assemblages could be generalized beyond a local context.

The aim of this study was to investigate response patterns of supralittoral arthropods associated with wrack deposits over several sandy beaches. For this, we evaluated the standing crop of wrack and their associated fauna on six sandy beaches, which differ in wrack composition and morphodynamics characteristics, located at Brazilian and Spanish Atlantic coasts. We predicted: 1) differences would be found between beaches with respect to total amount and their relative deposition on tide lines (i.e. bands); 2) differences would be found between wrack deposits in which relative ages vary with respect to density, diversity, and structure of invertebrate assemblages; 3) disregarding species differences, there would be similar patterns of the distribution of supralittoral assemblages as a response of the relative age of wrack deposits of sandy beaches located on both sides of the Atlantic Ocean.

MATERIALS AND METHODS

Study area

This study was conducted on six sandy beaches located in three geographical regions (Fig. 1): South (Paraná-PR) and Southeast (Rio de Janeiro-RJ) of Brazil and Southwest of Spain (SW Spain), in order to obtain, in a general way, similar patterns of wrack accumulation and distribution of arthropods assemblages inhabiting upper-wrack deposits. These regions were selected according to the type of allochthonous subsidies. The beaches of Paraná region were subsidized mainly by mangrove propagules, while the beaches of Rio de Janeiro and Southwest of Spain were subsidized mainly by macrophytes and macroalgae.

The coast of the Paraná region (PR) has a humid subtropical climate with a mean annual temperature of 22.2°C and mean annual precipitation of 1890 mm. Tides on the Paraná coast are semidiurnal and microtidal, with a tidal range between 0.5 and 2 m (Knoppers et al., 1987). Cem (25°34’24’’S; 48°20’ l3’’W) located near to the mouth of the Paranaguá bay estuary, is a low-energy reflective beach, modified by tides. It is has fine sands, a gentle slope and a low wave height. Assenodi (25°35’24”S; 42°22’04”W) located at Leste coastal plain, is an intermediate to dissipative, wave-dominated beach with medium sands and a gentle slope (Table S1). Both beaches are bordered by *restinga* (i.e. coastal sand dune vegetation).

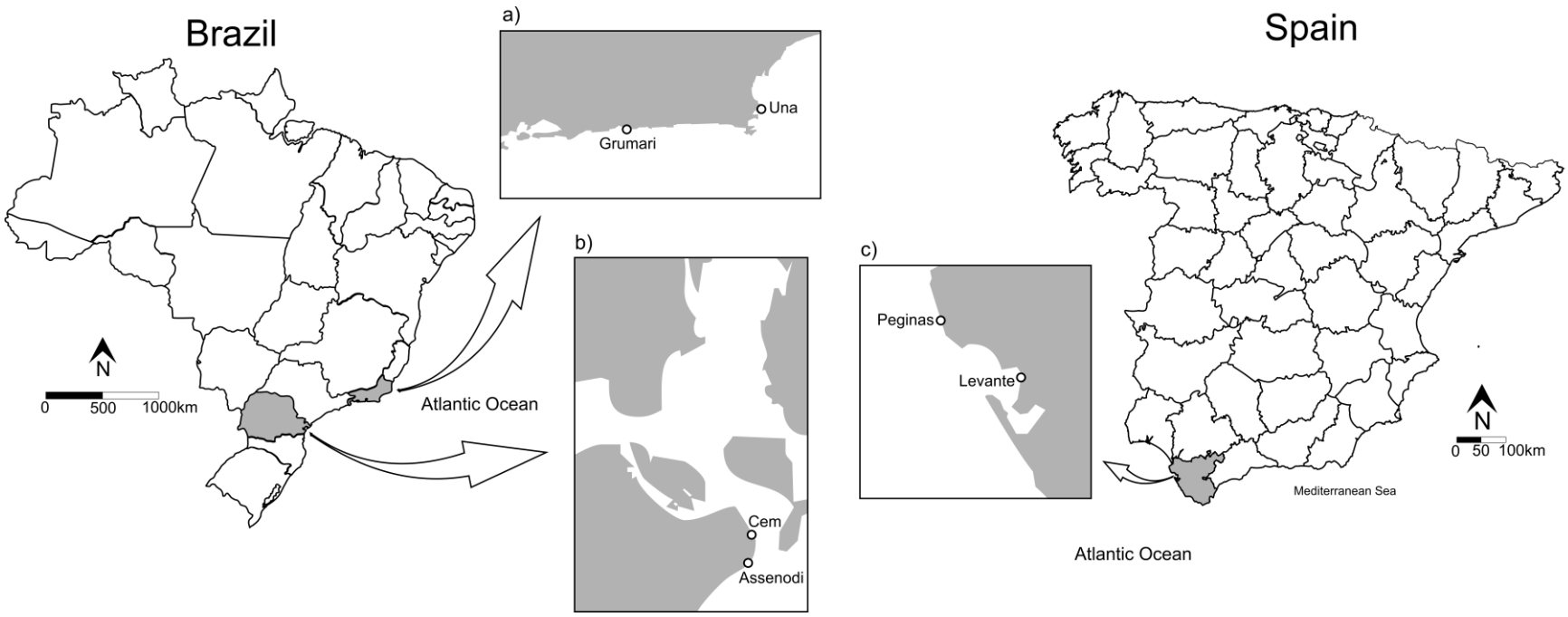

Figure 1. Location of sandy beaches surveyed at South (Paraná-PR) and Southeast (Rio de Janeiro-RJ) of Brazil and Southwest of Spain (SW).

The coast of Rio de Janeiro (RJ) has a semi-humid tropical with an annual average temperature of 22.2°C and average annual precipitation of 1890 mm. This region has microtidal, mixed semidiurnal tides, with a range between 0.3 and 0.7 m (Dias and Kjerfve, 2009). Grumari (23°02'52''S; 43°31'18''W), located in the west of Rio de Janeiro coast, is a dune-backed, high-energy reflective beach, classified as wave-dominated, with coarse sands and a steep slope. Una (22°43'02''S; 41°59'07''W), protected by Cape Búzios, classified as dissipative and wave-dominated beach, has fine sands with a gentle slope and is bordered for much of its length by restinga (Table S1).

The southwest of Spain (SW Spain) coast has a dry-summer subtropical climate with a mean annual temperature of 18.4°C and mean annual precipitation of 546.1 mm. The Gulf of Cadiz is a semidiurnal mesotidal environment with a tidal range between 3.2 and 1.1 m (Benavente et al., 2002). Levante (36°33'37''N; 6°13'27''W) located in the outer zone of Cadiz Bay, is a dune-backed, dissipative beach. It is characterized by medium sand, gentle slope and low wave heights. Peginas (36°39'43''N; 6°24'15''W) located at north of the Cadiz Bay, is classified as intermediate beach, backed by low cliffs and faced by rocky shore platform. It is wave-dominated, with medium sands and a moderate slope (Table S1).

Study design and sampling methods

All beaches were sampled on three consecutive days between 23 and 25 of February in the Paraná and Rio de Janeiro regions and between 29 and 31 of August in Southwest of Spain region. During these months, climatic conditions were quite similar (Table S1) and densities of the dominant species are usually high during summer months in the three regions (e.g. Caldas and Almeida, 1993; Souza and Gianuca, 1995; Cardoso and Veloso, 1996; Schreiner and Ozorio, 2003; Veloso et al., 2003; Gonçalves and Marques, 2011). Furthermore, samplings were carried out during spring tides, when large amounts of beach cast material and presence of wrack deposits along a well-defined lines or bands were expected (Ochieng and Erftemeijer, 1999). Therefore, in this study band is defined as the line parallel to the line tide covered of wrack. Wrack deposits stranded on beaches during the last highest spring tide and located above the current high-tide line were called the upper band. Meanwhile the lower band was formed at the last high tide and located at the current driftline. Generally, upper bands were composed of aged wrack, desiccated by exposure to air and sun for several days, while lower bands were

composed of fresh material deposited during the last high tide previous to the samplings (Orr et al., 2005; Jaramillo et al., 2006).

The sampling points were randomly designated along the upper and lower band of wrack deposits. The along-shore distance of the sampling area was 50 m. At each band, 18 samples were randomly collected, using a core of 15 cm diameter to penetrate the sediment to 10 cm in depth. At the free end of the corer, a plastic bag was used to prevent mobile fauna (mainly insects and amphipods) from escaping. This sampling design yielded a total sampling area of 0.70 m^2 and a total of 36 samples at each beach. All samples were preserved in 10% neutralized formalin. In the laboratory, wrack debris was washed and sieved through a 0.5 mm mesh. The macrofauna retained were sorted and identified to the lowest possible taxonomic level. Species number, density (expressed as total number of individuals per square meter) and diversity (Shannon–Wiener index) were calculated for each sample. Relative composition (measured as a percentage of each organic material) and the dry weight (g/m^2) of wrack were determined for each sample after drying at 60ºC.

The following environmental variables were recorded at each beach: slope estimated using Emery's profiling technique (Emery, 1961); beach width, measured as the distance between the base of the dune and the lower swash level; mean grain size (Folk and Ward, 1957); wave height was visually recorded and wave period was estimated with a stopwatch. These measurements were used to calculate the following indices that describe beach morphodynamic state: Dean's parameter (Ω) (Short and Wright, 1983) and relative tide range (RTR) (Masselink and Short, 1993).

Data analysis

Because our main goal was to search for patterns of wrack accumulation and distribution of supralittoral assemblages in the upper-shore, univariate and multivariate analyses were performed separately for each region (PR, RJ and SW). Differences in the amount of wrack were tested using orthogonal two-way ANOVA. Beach (with 2 levels) and bands (with 2 levels) were fixed factors. Moreover, differences in total density (ind. m^{-2}), species richness and diversity were also analysed following the same model. For the analyse of the invertebrate community structure on each beach, a matrix of biological data was ordered (nMDS) using Bray-Curtis's similarity index (Clarke and Warwick, 1994) and differences among beaches and bands were tested using a two-way Permutational Analysis of Variance (PERMANOVA, Anderson, 2001). Only significant

effects ($p<0.05$) were further investigated through a series of *a posteriori* pair-wise comparisons. To gauge the contribution of individual species to overall dissimilarity in community structure among beaches and bands, the similarity percentage routine (SIMPER) was used (Clarke and Warwick, 1994**)**. Differences in densities of main representative families were tested using a two-way ANOVA, with beach and band as fixed factors.

Before ANOVAs, the normality and homogeneity of variances of all dependent variables were assessed by Shapiro-Wilk and Cochran tests (Underwood, 1997), respectively. Untransformed data were used when transformations failed to stabilize heterogeneous variances, but in those cases, to reduce the chance of Type I error, the level of significance (α) used was 0.01 (Underwood, 1997). When significant results were found, *a posteriori* multiple comparisons were made using the Student-Newman-Keuls (SNK) test ($\alpha = 0.05$).

RESULTS

Beach wrack deposits

Wrack composition was different in each studied region. Wrack deposits of Paraná region were composed of mangrove propagules dominated by *Laguncularia racemosa* (60%), followed by *Avicennia schaueriana* (20%) and *Rhizophora mangle* (20%). More than 60% of the wrack on Una (RJ) was composed of macroalgae (*Sargassum furcatum* var. *humilis* and *Osmundaria obtusiloba*) and 40% by aquatic macrophytes (*Typha domingensis* and *Salvinia* sp.), while in Grumari (RJ), dead invertebrates (crustaceans, mollusks and insects) and macroalgae (*Ulva* sp. and *Sargassum* sp.) accounted for 74% and 36%, respectively. On the other hand, the driftlines of beaches in SW Spain were composed of macroalgae and seagrass. In particular, wrack deposits collected at Levante were composed of two seagrasses species: *Cymodocea nodosa* (65%) and *Zostera noltii* (35%). Meanwhile at Peginas the deposits were a mixture of red and brown macroalgae: *Halopithys incurva* (82%), *Jania* sp. (8%), *Halopteris scoparia* (6%) and *Cladostephus spongiosus* (4%).

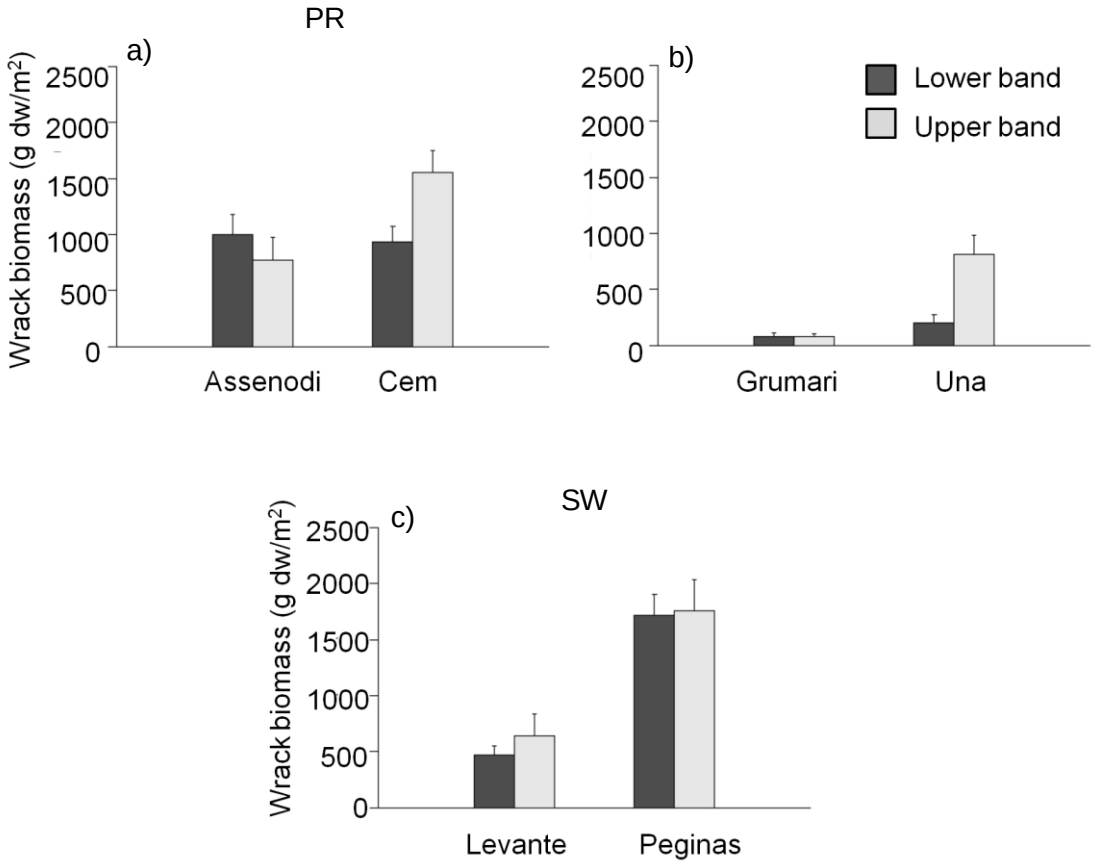

Figure 2. Mean (±standard error, n = 18) dry weight wrack material (g.m^{-2}) on beaches of three regions: a) Assenodi and Cem on Paraná region – PR; b) Grumari and Una on Rio de Janeiro region – RJ and c) Levante and Peginas on Southwest of Spain region–SW.

In the Paraná region, the dry weight of wrack varied significantly between beaches but this variation differed between bands (i.e. significant Beach x Band interaction, Table 1). The amount of wrack deposited on the upper band was significantly greater on Cem than on Assenodi (SNK, $p < 0.05$; Fig. 2a). Moreover, this variable did not differ between bands in Cem and Assenodi (SNK, $p > 0.05$). In the Rio de Janeiro region, the amount of stranded wrack also differed between beaches and bands (i.e. Beach x Band interaction, Table 1). The amount of wrack deposited on both bands was greater at Una than at Grumari (SNK, $p < 0.05$; Fig. 2b). Moreover, the dry weight of wrack was significantly higher on the upper than on the lower band, only at Una beach (SNK, $p < 0.05$). In the SW Spain, the quantity of wrack differed only between beaches (Table 1). Peginas registered significantly higher values for the amount of wrack than did Levante (SNK, $p<0.05$; Fig. 2c).

Table 1 Results from two-way ANOVA, showing differences in dry weight wrack, total density, species richness and diversity index between wrack bands (two levels; fixed factor) and beaches (two levels; fixed factor) in each geographical region (Paraná-PR, Rio de Janeiro-RJ and southwest of Spain-SW, respectively). Results from PERMANOVA analysis on invertebrate assemblage structures were showed, following same sources of variation for each region. Degrees of freedom (df) and Pseudo-F are shown. The data are fourth root transformed. ***p < 0.001; **p < 0.01;*p < 0.05.

		PR			RJ			SW	
Source	df	MS	F	df	MS	F	df	MS	F
Wrack									
Beach	1	7.51	6.01*	1	18.61	36.0***	1	32.00	58.79***
Band	1	0.17	0.14	1	3.49	6.76*	1	0.00	0.00
Beach x band	1	6.36	5.09*	1	2.42	4.69*	1	0.14	0.26
Residual	68	1.25		68	0.52		68	0.54	
Total density					a				
Beach	1	1912.43	27.93***	1	22033230.00	15.67**	1	34.56	6.78*
Band	1	91.85	1.34	1	9862520.00	7.02	1	10.09	1.98
Beach x band	1	88.79	1.29	1	1885634.00	13.43**	1	2.70	0.53
Residual	68	68.49		68	1405397.00		68	5.10	
Species richness								a	
Beach	1	0.47	18.17***	1	6.13	6.23*	1	1.68	1.76
Band	1	0.00	0.08	1	42.01	42.74***	1	0.35	0.36
Beach x band	1	0.07	2.58	1	17.01	17.31***	1	0.13	0.13
Residual	68	0.03		68	0.98		68	0.95	
Diversity									
Beach	1	0.72	4.67*	1	0.21	1.71	1	0.40	1.60
Band	1	0.15	0.95	1	5.25	43.09***	1	0.98	3.89
Beach x band	1	0.47	3.09	1	0.15	1.22	1	0.14	0.56
Residual	68	0.15		68	0.12		68	0.25	
Source	df	MS	Pseudo-F	df	MS	Pseudo-F	df	MS	Pseudo-F
Assemblages									
Beach	1	42015.00	31.33***	1	4841.80	41.05**	1	11002.00	65.18***
Band	1	5742.10	42.82***	1	4849.70	41.12**	1	14658.00	86.84***
Beach x band	1	7631.10	56.91***	1	24023.00	20.37**	1	2872.90	17.02
Residual	68	91186.00		68	1179.30		68	1687.90	

a Cochran test no significant.

Effect of wrack bands on supralittoral arthropods

Composition and faunal descriptors of supralittoral arthropods

In the Paraná region, 382 individuals belonging to 8 taxa were sampled in wrack deposits in both beaches. The tenebrionid *Phaleria testacea* and Nitidulids were the most abundant taxa at Cem, while the staphylinid *Bledius bonariensis* and the talitrid *Platorchestia monodi* were the most representative species at Assenodi. On the other hand, 1228 individuals belonging to 16 taxa were found in beach debris in Rio de Janeiro region (Table S2). Wrack deposits of Una and Grumari were dominated by the amphipods *Talorchestia tucurauna* and *Atlantorchestoidea brasiliensis*, respectively, while other groups (Isopoda, Diptera, Heteroptera and Araneae) showed low contributions to the total abundance of both beaches (Table S2). In SW Spain, 420 individuals classified in 17 taxa were collected. Seagrass wrack of Levante was dominated by the talitrid *Talitrus saltator* and tenebrionid *Phaleria bimaculata*, while staphylinids followed by *Talitrus saltator* and *Phaleria bimaculata* were the most abundant taxa in macroalgal wrack of Peginas (Table S2).

In the Paraná region, total density, species richness and diversity index differed between beaches (Table 1). These biological attributes were higher on Assenodi than on Cem (SNK; $p < 0.05$; Fig. 3a, b, c). In the Rio de Janeiro region, total density and species richness varied among bands and beaches (i.e. significant Beach x Band interaction; Table 1). Both variables were significantly higher in the upper band of Una than in Grumari (SNK; $p<0.05$). Moreover, Una showed differences between bands, with higher values in the upper than lower band (SNK; $p<0.05$; Fig. 4 a, c). By contrast, diversity index only differed between bands (Table 1), with higher diversity in upper than in the lower band at both beaches (SNK; $p < 0.05$; Fig. 4b). In SW Spain, total density differed between beaches (Table 1), with higher values on Levante than on Peginas (SNK; $p < 0.05$; Fig. 5a). Nevertheless, the diversity index and species richness proved similar among bands and beaches (Fig. 5b, c).

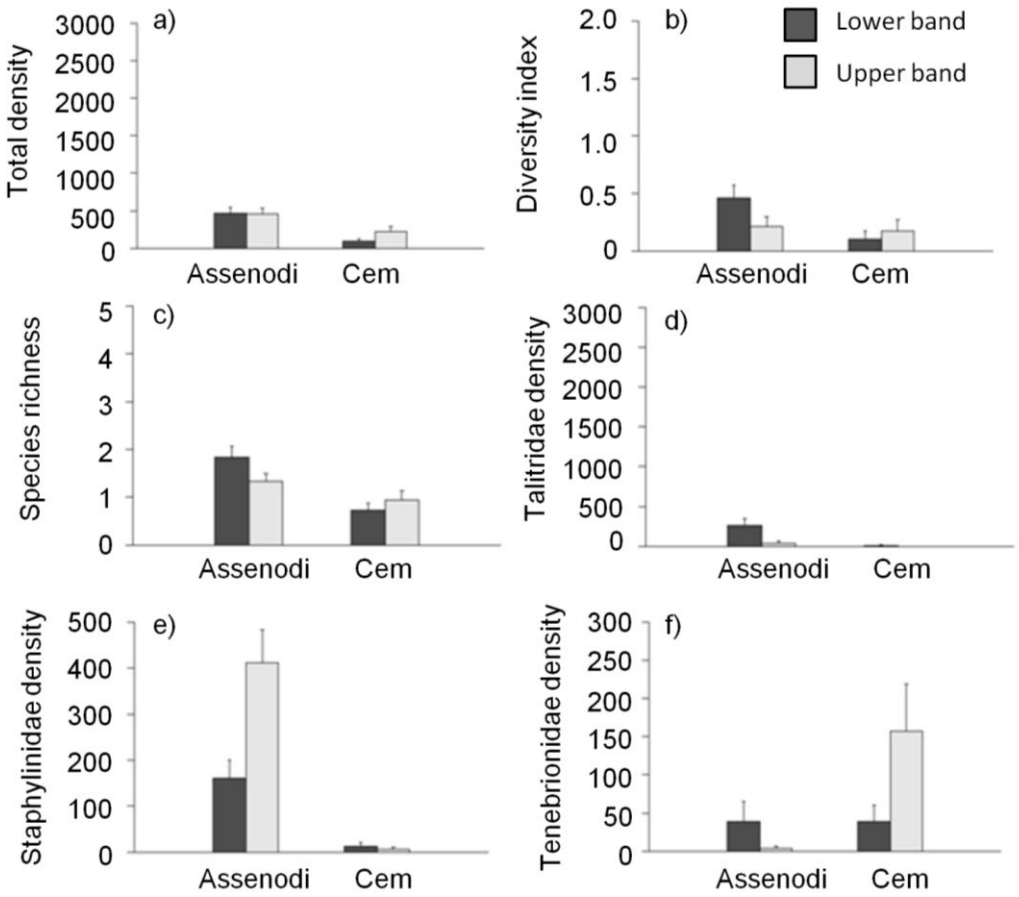

Figure 3. Mean (±standard error, n = 18) (a) total density (nº indv. m^{-2}), (b) diversity index (Shannon-Wiener), (c) species richness and density (nº indv. m^{-2}) of three main families: (d) Talitridae, (e) Staphylinidae and (f) Tenebrionidae on beaches of Paraná region (Assenodi, Cem).

Analysis of invertebrate assemblages

In three regions (PR, RJ and SW), invertebrate assemblages structure varied between upper and lower wrack bands (Fig. 6), but this variation was not consistent over beaches (Table 1, PERMANOVA results). *Post hoc* comparisons showed that assemblages structure differed among wrack bands ($p<0.05$) on Assenodi (PR), Una (RJ), Peginas and Levante (SW Spain). SIMPER analysis showed that Talitridae contributed at least 40% of total dissimilarity among upper and lower bands on these four beaches. Staphylinidae contributed 35%, 30% and 27% of total dissimilarity between bands on Assenodi, Una and Peginas, respectively. Moreover, Tenebrionidae accounted for 13%, 39% and 26% of total dissimilarity between bands on Assenodi, Una and Levante,

respectively. However, assemblage structures on Cem (PR) and Grumari (RJ) did not show significant differences between bands ($p>0.05$; Fig. 6 b, c).

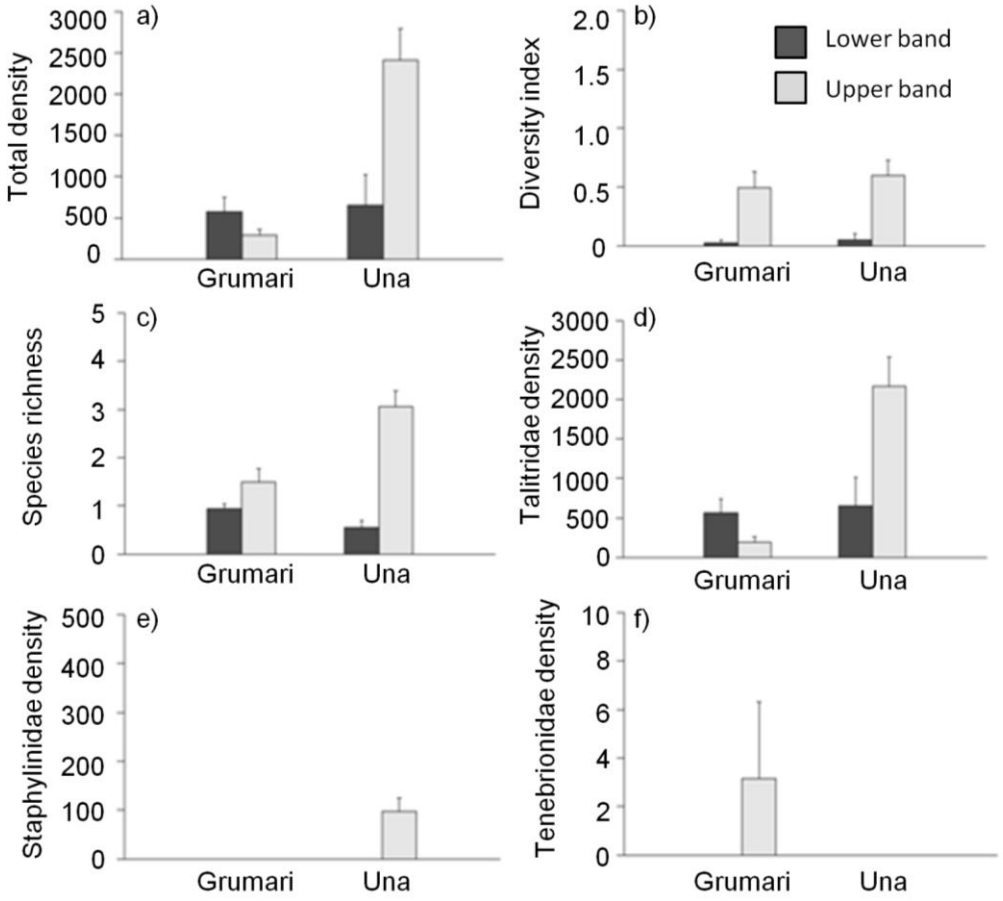

Figure 4. Mean (±standard error, n = 18) (a) total density (nº indv. m^{-2}), (b) diversity (Shannon-Wiener), (c) species richness and and density (nº indv. m^{-2}) of the three main families: (d) Talitridae, (e) Staphylinidae and (f) Tenebrionidae on beaches of Rio de Janeiro region (Grumari and Una).

In general, the accumulation of wrack in two different bands had an effect on the distribution of the species belonging to three most representatives families (Talitridae, Staphylinidae and Tenebrionidae), but their densities differed between beaches in each region. In the Paraná region, Talitridae, Staphylinidae and Tenebrionidae differed between bands, but this variation was not consistent between beaches (i.e. significantly Beach x Band interaction; Table 2). Talitrids were found only in the lower band at Cem (Fig. 3d) Moreover, their density was significantly higher in the lower than in the upper band at Assenodi (SNK, $p<0.05$; Fig. 3d). Staphylinidae density was significantly higher in the upper than in the lower band only at Assenodi (SNK, $p<0.05$; Fig. 3e).

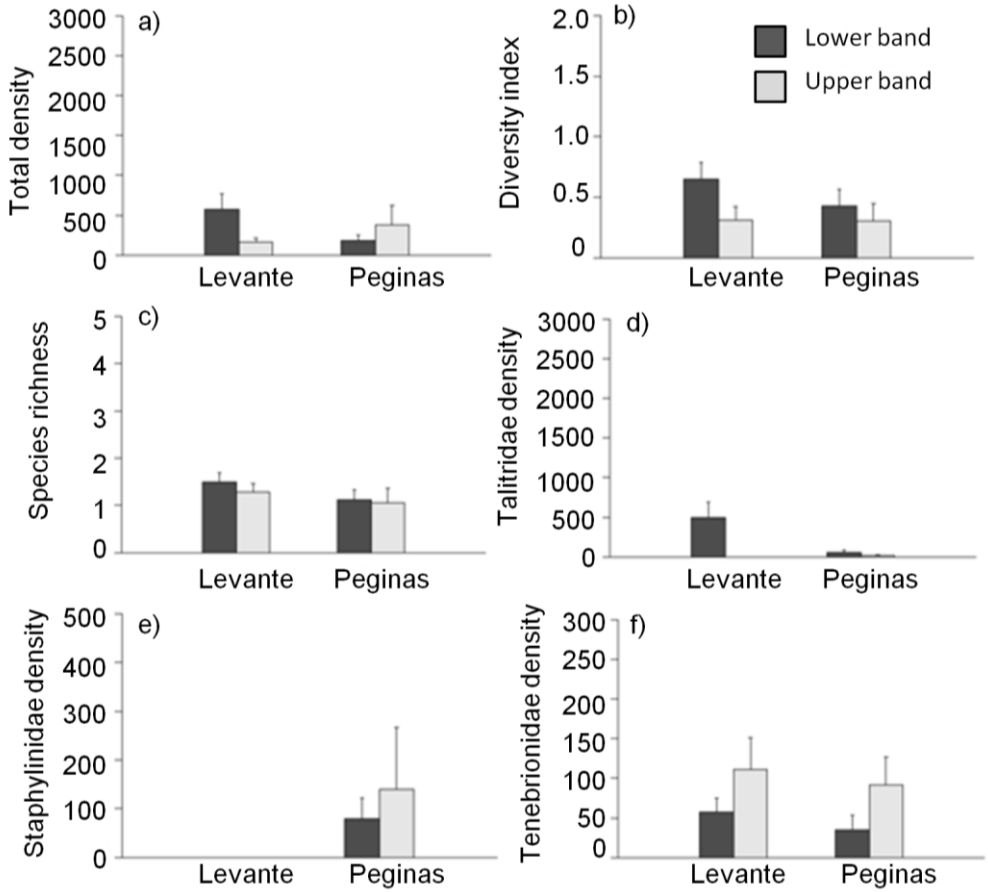

Figure 5. Mean (±standard error, n = 18) (a) total density (nº indv. m^{-2}), (b) diversity (Shannon-Wiener), (c) species richness and density (nº indv. m^{-2}) of the three main families: (d) Talitridae, (e) Staphylinidae and (f) Tenebrionidae on beaches Spain region (Levante and Peginas).

On the other hand, Tenebrionidae density was significantly higher in the upper than in the lower band only at Cem beach (SNK, $p<0.05$; Fig. 3f). In the Rio de Janeiro region, the density of Talitridae varied significantly between wrack bands, although this variation was not consistent across beaches (i.e. significant Beach×Band interaction; Table 2). Talitrids density was significantly higher in the lower than the upper band at Grumari, while Una showed the opposite pattern (SNK, $p<0.05$; Fig. 4d). Staphylinids were found only at Una, while tenebrionids only at Grumari, and therefore it were not possible to test differences between bands and beaches. However, both Coleopteran families were found in the upper bands in both beaches (Fig. 4e, f). In Southwest of Spain, Talitridae density varied significantly between wrack bands (Table 2), with higher density in lower than upper band in both beaches (SNK, $p<0.05$; Fig. 5d) Staphylinidae and Tenebrionidae density did not show significant differences between

bands consistently between beaches (i.e. no significant interaction; Table 2). Staphylinidae density was greater at upper than at lower band, but only at Peginas (SNK, $p<0.05$; Fig. 5e). However, tenebrionids appeared to occupy mainly the upper band on both beaches (Fig. 5f).

Table 2 Results from two-way ANOVA, showing differences in density of main families (Talitridae, Staphylinidae and Tenebrionidae) between wrack bands (two levels; fixed factor) and beaches (two levels; fixed factor) in each geographical region (Paraná-PR, Rio de Janeiro-RJ and Southwest of Spain-SW). If a family was absent in one of bands or beaches, no statistical tests were applied and it is indicated with a dash (-). ***p < 0.001; **p< 0.01;*p < 0.05; $^{+}$ 0.05<p<0.06.

		PR			RJ			SW	
Source	df	MS	F	df	MS	F	df	MS	F
Talitridae			a						a
Beach	1	380671.00	10.95**	1	7.89	5.92*	1	814331.00	4.59*
Band	1	242263.00	6.97*	1	3.99	2.99	1	1310658.00	7.39**
Beach x band	1	203047.00	5.84**	1	37.61	28.24***	1	914467.00	5.16*
Residual	68	2363130.00		68	1.33		68	177340.00	
Staphylinidae									a
Beach	1	274.03	78.59***	-	-	-	1	215918.00	2.70
Band	1	13.10	3.76	-	-	-	1	16372.00	0.20
Beach x band	1	22.52	6.46*	-	-	-	1	16372.00	0.20
Residual	68	3.48		-	-	-	68	79939.00	
Tenebrionidae									
Beach	1	28.59	6.46*	-	-	-	1	2.60	2.37
Band	1	2.54	0.57	-	-	-	1	3.58	3.26^{+}
Beach x band	1	35.25	7.97*	-	-	-	1	0.37	0.34
Residual	68	4.42		-	-	-	68	5.82	

a Cochran test no significant.

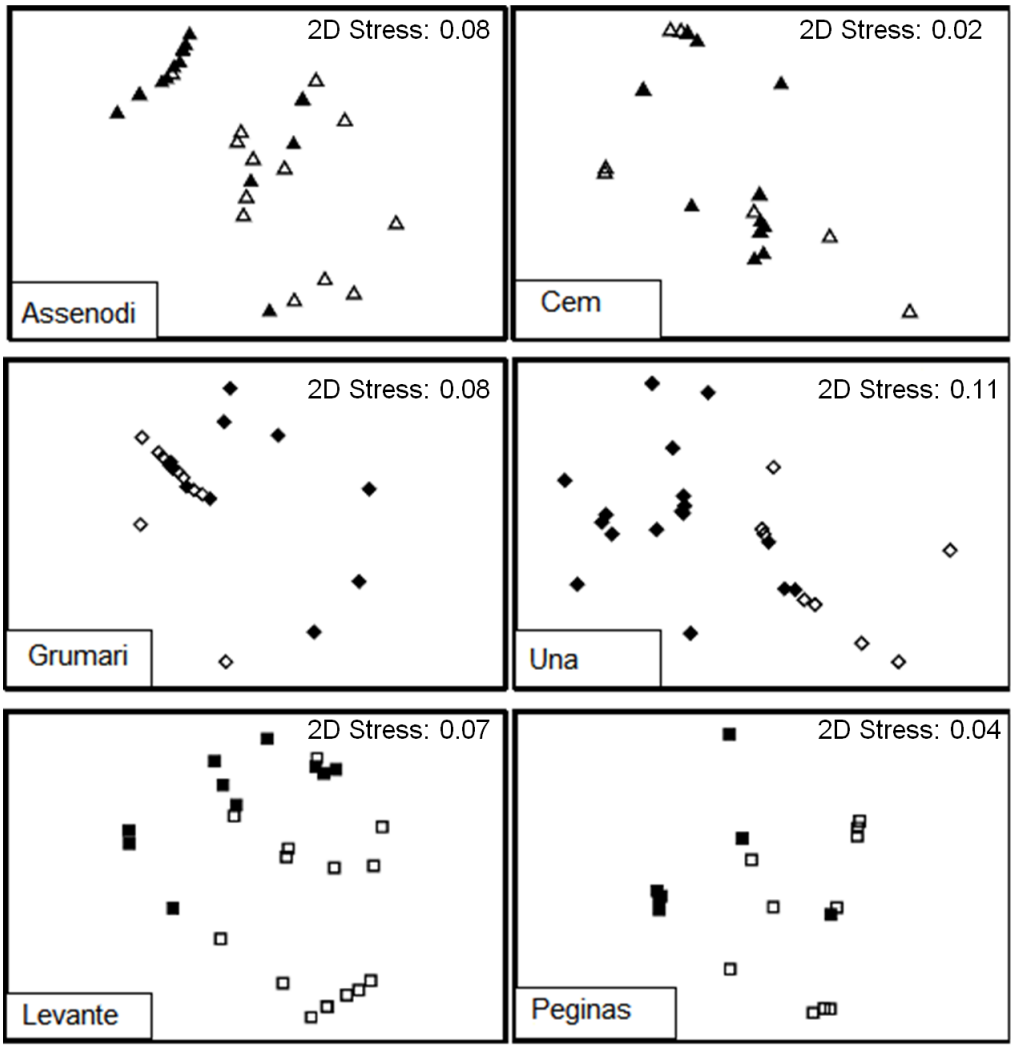

Figure 6. Non-metric multidimensional scaling (nMDS) for differences of assemblages between upper and lower wrack bands at each beach: Assenodi (a) and Cem (b) on Paraná region; Grumari (c) and Una (d) on Rio de Janeiro region and Levante (e) and Peginas (f) on Southwest of Spain region.

DISCUSSION

Differences on wrack deposition between beaches

The composition and amount of wrack deposited at a given beach is determined largely by the offshore marine environment such as prevailing winds, current directions, waves and tides that determine the exposure to water motion; nearshore sources; coastal topography and the physical characteristics of detritus (e.g. buoyancy) (Ochieng and Erftemeijer, 1999; Orr et al., 2005; Barreiro et al., 2011). In the present study, the composition of wrack deposits differed in all the regions studied. Wrack was composed

mainly of mangrove fruits, seeds and leaves in the Paraná region, aquatic macrophytes, macroalgae as well as, in lesser proportion, dead invertebrates in the Rio de Janeiro region and macroalgae and seagrass in southwest Spain region. Although macroalgae and seagrass, are described as the principal organic components of beach-cast material (Colombini and Chelazzi, 2003), mangrove debris are notable on tropical and subtropical beaches and sandy coast near estuarine systems (Lugo and Snedaker, 1974), as in the Paraná region. In this region (PR), beaches located along and near the estuarine system of Paranaguá Bay are subsidized by mangrove propagules and marsh macrodetritus (Rosa et al., 2007; Borzone and Rosa, 2009).

A high variability was detected in the amount of stranded wrack among beaches in the three study region. Cem, Una and Peginas had higher values of dry weight of beach debris than Assenodi, Grumari and Levante, respectively. It appears that some of this variation was related to different morphodynamic states of beaches, which differ its placements on the coast. Cem (PR) is near to the mouth of a estuary, Una (RJ) is near to a rocky headland and Levante (SW Spain) is near to an ocean bay. Thus, these beaches had low wave heights, high RTR values and gentle slopes, features which could create favourable conditions for stranding wrack. In fact, a recent study has demonstrated that stranding of algal wrack is favored in wave-protected environments due to the influence of low waves energy on the beach front that causes a reduction in the flow of water in this locations. (Barreiro et al., 2011). Moreover, the spatial variability (i.e. between beaches) in the amount of wrack could be related to the presence and proximity of productive adjacent habitats such as mangroves, rocky intertidal and rocky shore near Cem, Una and Peginas, respectively. These habitats are source of drift materials and therefore, it is probably that these beaches (i.e. Cem, Una and Peginas) received more amount of wrack than the other beaches studied. In fact, in other coastal regions, beaches near areas with high production of macroalgae or/and seagrass receive extensive wrack inputs (Stenton-Dozey and Griffiths, 1983; Mateo, 2010). However, it is important to keep in mind that the dry weight of wrack used to estimate the subsidies in the present study represents the standing crop, not the actual input or turnover rates of the wrack. In fact, wrack inputs on sandy beaches vary greatly in space and time and depend on complex interactions among coastal topography and different physical factors such as waves, currents, winds, etc. (Polis et al., 2004).

Effect of wrack bands on supralittoral arthropods

This study is the first to analyse the composition of wrack-associated fauna on geographically distant sandy beaches subsidized by different types of allochthonous materials. The results indicate that different types of stranded material i.e. macrophytes, macroalgae as well as mangrove propagules and carrion provide a physical structure, which can be used as shelter or breeding sites, and a food source by supralittoral arthropods (Inglis, 1989; Colombini et al., 2000; Jedrzejczak, 2002b; Ince et al., 2007).

The major components of wrack deposits, disregarding species differences, were talitrids followed by tenebrionids and/or staphylinids, which accounted for approximately 80% of the communities. However, their relative contributions varied in each region. In Rio de Janeiro region, wrack deposits were dominated by talitrid amphipods, as shown by previous studies in other regions of the world (e.g. Behbehani and Croker, 1982; Robertson and Lucas, 1983; Lavoie, 1985; McLachlan, 1985; Mardsen, 1991). Although, in Paraná and Southwest of Spain regions, coleopterans (tenebrionids and staphylinids) and talitrids were abundant on stranded material, as elsewhere (e.g. Colombini et al.,1998, 2000; Dugan et al., 2003; Jaramillo et al., 2006; Olabarria et al., 2007).

Density, species richness and diversity differed between beaches from Paraná and Rio de Janeiro regions, while only total density varied between beaches of Southwest of Spain. Although differences in the amount of deposited wrack were found between beaches in each region, density, species richness and diversity did not differ in the same way (i.e. beaches with high amount of wrack did not have high density in all the cases). A positive relationship between the amount of wrack and community attributes (density, species richness, and biomass) had reported in previous studies (e.g. Dugan et al., 2003; Gonçalves et al., 2009; Gonçalves and Marques, 2011). However, our results did not show this pattern of variation. Therefore, it is possible that physical and environmental features (e.g. grain size, shoreline types, degree of exposure) of each beach might also explain the differences in community attributes. On the other hand, no differences were found between upper and lower wrack bands in biological attributes, except on Una beach. However, wrack bands had an effect on assemblage structures in most of the beaches studied. This presumably related to differences in location, and therefore, in moisture and state of decomposition of wrack bands, which influence the distribution and zonation of arthropod assemblages (Griffiths and Stenton-Dozey, 1981;

Inglis, 1989; Marsden, 1991; Colombini and Chelazzi, 2003; Jaramillo et al., 2006; Ince et al., 2007).

Despite the variability of Talitridae density between beaches, talitrids (*Atlantorchestoidea brasiliensis*, *Platorchestia monodi* and *Talitrus saltator*) dominated lower wrack bands on most of the beaches studied. In general, lower bands were located at the most recent driftline (i.e. at the height of high tide line) and composed of newly stranded material. Previous studies have reported that talitrid amphipods have a closer association with new than aged algal wrack deposits (Marsden, 1991; Jedrzejczak, 2002b; Jaramillo et al., 2006). Our results confirm that this association in algal wrack and other types of beach-cast material such as mangrove propagules and carrion, which has not been reported in previous studies. *A. brasiliensis* and *T. saltator* are found mainly on the supralittoral zone of exposed beaches (e.g. Souza and Gianuca, 1995; Veloso et al., 1997; Veloso and Cardoso, 2001; Colombini et al., 2002; Marques et al., 2003; Veloso et al., 2003; Gonçalves and Marques, 2011), while *P. monodi* prefer protected beaches, occurring mainly in estuarine beaches and mangrove swamps (Morino and Ortal, 1995). The occurrence of *P. monodi* on an exposed beach, such as Assenodi in the Paraná region, suggests the expansion of its spatial distribution. In this case, the mangrove propagules from the estuarine system of the Paranaguá Bay could be an effective dispersal mechanism as mentioned by Rosa et al. (2007) and Borzone and Rosa (2009).

Talorchestia tucurauna showed the opposite pattern with respect to the other talitrid species i.e. higher density on upper than on lower band. This might be related to the physical characteristics of Una beach such as flat slope, fine sediment and a narrow intertidal, which facilitate events of flooding above the upper band during spring high tides (personal observation). These flood events could have moistened upper wrack deposits and making them wetter than the lower deposits, a situation that may explain the high density of *T. tucurauna* on the upper band of this beach. In fact, available moisture is one of the most important factors in determining the distribution of talitrid species (Marsden, 1991), so that individuals may select wrack deposits based on the risk of desiccation stress.

Tenebrionids and staphylinids species were found mainly on upper wrack deposits. We hypothesised that their spatial distributions may be related to the different susceptibility to dehydration of these taxa. The presence of tenebrionids species on the studied beaches might be related to the preference for aged and dry wrack deposits as

had been reported for different species of genus *Phaleria* (Colombini et al., 2002; Jaramillo et al., 2006). In fact, Aloia et al. (1999) demonstrated in a laboratory experiment that tenebrionids preferred extremely dry sands (0-2.5%). On the other hand, Staphylinidae species are very sensitive to dehydration (Colombini et al., 1998; Garrido et al., 2008), so it is possible that they have been found under wrack deposits that presented some water content. Preliminary results of a laboratory experiment indicated that *Bledius bonariensis* preferred sands with medium moisture level (5-10%) against extremely dry (0%) or wet sediments (15-20%) (unpublished data).

The value of a food resource for a consumer may depend on its state of decomposition, which affects its water content, toughness, nutritional value and relative content of secondary metabolites (Pennings et al., 2000; Crawley and Hyndes, 2007; Poore and Gallagher, 2013). Therefore, the distribution of taxa studied could be influenced by their metabolic needs and the quality of allochthonous food resource. For example, talitrid amphipods dominated the lower wrack band in most of the beaches studied; this may be related to their preference for fresh rather than aged stranded wrack such as food (Colombini et al., 2000; Lastra et al., 2008; Duarte et al., 2010). This response pattern was noted in beaches subsidized by different types of allochthonous materials (i.e. mangrove propagules, carrion, macrophytes, and macroalgae). Several authors have reported that talitrid amphipods feed on algal wrack (e.g. Crawley and Hyndes 2007; Duarte et al., 2010; Lastra et al., 2008; Olabarria et al., 2009). However, recently Veloso et al. (2012) have demonstrated that *Atlantorchestoidea brasiliensis* can consume animal material, such as fragments of crabs, molluscs and dead insects besides fresh macroalgae. This might explain the unexpected high density of talitrid amphipods in the lower band of Grumari, the beach with the lowest amount of algal wrack but with presence of dead invertebrates in the driftlines. This suggests that talitrid amphipods do not depend on a specific subsidy, and therefore, reflecting flexible foraging strategies when comparing populations that inhabit different types of wrack. In fact, Brown (1996) suggested that behavioural plasticity is directly related to population survival on sandy beaches. In this study, only relative age of wrack deposits, which differ in their position in the supralittoral zone, was used as explanatory variable. However, freshness, nutritional quality and microclimatic conditions of wrack deposits are pausible explanatory variables and should be measured in future studies.

In summary, our results suggest that supralittoral arthropods, mainly species of Talitridae, Staphylindiae and Tenebrionidae can inhabit different types of stranded

materials on sandy beaches. Moreover, the results reflect that the distribution pattern and, therefore, the relative age of wrack deposits influence the structure of upper-shore assemblages. This influence was detected in the density of the dominant taxa and their distribution in wrack bands; that is: species of talitrid amphipods inhabit the lower band, while staphylinid and tenebrionid species occupy the upper band of wrack. However, more studies are needed to understand how habitat traits (e.g. food quality, microclimatic conditions) as well as behavior, feeding strategies and trophic relationships between species influence the association between arthropods species and wrack on beaches worldwide. In this regard, comparative studies of supralittoral arthropods assemblages could be relevant in the search of ecological equivalents inhabiting wrack deposits.

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SUPLEMENTARY MATERIAL

Table S1 Summary of climate data (temperature and precipitation, mean 1961-1990) of each region (Paraná– PR; Rio de Janeiro – RJ and Southwest of Spain – SW). Physical characteristics including length and width, slope, Mz (mean sand grain size), T (wave period), Hb (wave height), Dean´s parameter, Tide (mean spring tide range), RTR (Relative Tide Range) of each surveyed beach Assenodi (Ass) and Cem; Una and Grumari (Gru); Levante (Lev) and Peginas (Peg).

Region	**PR**		**RJ**		**SW**	
	Maximun	Minimun	Maximun	Minimun	Maximun	Minimun
Temperature						
Month	February	July	February	July	August	January
Annual mean (ºC)	26.7	18.3	28.9	22.2	24.7	12.7
Precipitation						
Month	March	June	December	July	December	July
Total mean (mm)	300.0	80.0	137.2	45.7	104.1	0.0
Beach	**Ass**	**Cem**	**Gru**	**Una**	**Lev**	**Peg**
Beach length (m)	2100	1000	2000	2500	1000	1100
Intertidal width (m)	110	53	65	75	105	50
Slope (º)	2.48	2.20	4.30	1.20	1.00	1.81
Mz (Φ)	2.28	2.15	0.53	3.03	2.89	1.41
T (s)	7.00	4.90	12.10	9.12	5.00	7.73
Hb (m)	1.00	0.25	1.01	0.60	0.35	0.93
Dean (Ω)	5.53	1.76	0.77	5.47	4.96	2.22
Tide (m)	1.70	1.70	1.50	1.50	2.00	2.00
RTR	1.70	6.80	1.49	2.50	5.71	2.15

Table S2 Total abundance (nº indv.) and percent composition (% community) of arthropods collected in wrack deposits on beaches of each region (Paraná–PR; Rio de Janeiro – RJ and Southwest of Spain – SW).

		Beaches			
		Assenodi		Cem	
	Taxa	Nº indvs	%Community	Nº indvs	%Community
PR	**SubP. Crustacea**				
	Ord. Amphipoda, Talitridae				
	Platorchestia monodi (Stock, 1996)	92	23.29	3	2.38
	SubP. Hexapoda				
	Ord. Coleoptera				
	Tenebrionidae				
	Phaleria testacea (Say, 1824)	13	3.29	60	47.62
	Carabidae	3	0.76	-	-
	Cleridae	-	-	2	1.59
	Nitidulidae	-	-	28	22.22
	Eflagitatus	1	0.25	-	-
	Staphylinidae				
	Bledius bonariensis (Bernhauer, 1912)	174	44.05	-	-
	Bledius hermani (Caron and Ribeiro-Costa, 2007)	-	-	5	3.97
	Bledius fernandezi (Bernhauer, 1939)	1	0.25	-	-
	Larva bledius indet.	111	28.10	28	22.22
		Una		**Grumari**	
	Taxa	Nº indvs	%Community	Nº indvs	%Community
RJ	**SubP. Crustacea**				
	Ord. Amphipoda, Talitridae				
	Atlantorchestoidea brasiliensis (Dana, 1853)	-	-	238	87.50
	Talorchestia tucurauna (Müller, 1864)	894	91.88	-	-
	Ord. Isopoda				
	Tylidae				
	Tylos europaeus (Audouin, 1825)	2	0.21	-	-
	SubP. Chelicerata, Ord. Araneae				
	Araneae indet.	5	0.51	-	-
	SubP. Hexapoda				
	Ord. Coleoptera				
	Tenebrionidae				
	Phaleria testacea (Say, 1824)	-	-	6	1.45
	Hydraenidae	-	-	2	0.74
	Staphylinidae				
	Bledius indet.	31	3.19	-	-
	Lycidae	-	-	1	0.37
	Ord. Diptera, Subord. Nematocera				

	Culicoidea	2	0.21	-	-
	Muscoidea	1	0.10	-	-
	Sarcophagidae	-	-	7	2.57
	Ceratopogonidae	-	-	3	1.10
	Ord. Hymenoptera				
	Formicidae	21	2.16	15	5.51
	Ord. Hemiptera, Subord. Heteroptera				
	Tingidae	-	-	1	0.37
	Cydnidae	-	-	1	0.37
	Subord.Sternorrhyncha				
	Psyllidae	3	0.31	-	-

		Levante		**Peginas**	
	Taxa	Nº indvs	%Community	Nº indvs	%Community
SW	**SubP. Crustacea**				
	Ord. Amphipoda, Talitridae				
	Talitrus saltator (Montagu, 1808)	149	63.40	16	9.20
	Deshayesorchestia deshayesii (Audouin, 1826)	2	0.85	6	3.45
	Africorchestia spinifera (Mateus, 1962)	4	1.70	-	-
	Pseudorchestoidea brito (Stebbing, 1891)	2	0.85	-	-
	Ord. Isopoda				
	Tylidae				
	Tylos europaeus (Arcangeli, 1938)	-	-	1	0.57
	Sphaeromatidae				
	Sphaeroma serratum (Fabricius, 1787)	-	-	1	0.57
	SubP. Chelicerata, Ord. Araneae				
	Agelinidae	3	1.28	0	0.00
	SubP. Hexapoda				
	Ord. Coleoptera				
	Tenebrionidae				
	Phaleria bimaculata (Linnaeus, 1767)	53	22.55	40	22.99
	Carabidae	2	0.85		
	Histeridae	14	5.96	23	13.22
	Staphylinidae				
	Staphylinidae indet.	-	-	69	39.66
	Ord. Diptera, Subord. Nematocera				
	Canacidae	4	1.70	-	-
	Psychodidae	2	0.85	-	-
	Anthomyzidae	-	-	1	0.57
	Limoniidae	-	-	15	8.62
	Ord. Hymenoptera				
	Formicidae	-	-	1	0.57
	Ord. Hemiptera, Subord. Heteroptera				
	Mesoveliidae	-	-	1	0.57

DISTRIBUTION PATTERNS OF SUPRALITTORAL ARTHROPODS: WRACK DEPOSITS AS A SOURCE OF FOOD AND REFUGE ON EXPOSED SANDY BEACHES (SW SPAIN)

Distribution patterns of supralittoral arthropods: wrack deposits as a source of food and refuge on exposed sandy beaches (SW Spain)

ABSTRACT

Wrack deposits are a common feature of sandy beaches worldwide. Despite their relevance, the habitat features of wrack debris and their potential influence on the distribution of upper-shore arthropods remain poorly understood. In this study, the distribution of supralittoral arthropods was analysed by sampling areas covered and not covered by wrack on two tidal levels during winter and summer from two sandy beaches of south-western Spain. Despite the differences between beaches and seasons, density, species richness and diversity were significantly higher in wrack patches than in bare sand. Moreover, community structure and composition varied between both microhabitats, due to the influence of wrack deposits on the habitat selection by arthropods species. Food availability combined with temperature or moisture mostly explained the distribution pattern of assemblages. Moreover, these habitat features varied between wrack bands, the lower band being fresher and wetter than upper band. The density of the main species inhabiting wrack was correlated mainly with moisture. The present study provide evidences about the role of algal wrack structuring diversity and composition of supralittoral arthropods stressing the importance of the habitat heterogeneity to maintain abundant and diverse communities on exposed sandy beaches.

Keywords: wrack; season; supralittoral arthropods; habitat heterogeneity; microclimatic conditions; food availability

INTRODUCTION

Disturbance events are a major source of temporal and spatial heterogeneity structuring natural communities (Sousa, 1984). On sandy beaches, an important small-scale natural disturbance is the stranding of organic materials (wrack) from offshore algal beds and closer rocky intertidal shores (e.g. seaweeds, seagrasses) (Inglis, 1989; Rossi and Underwood, 2002; Colombini and Chelazzi, 2003). Stranded wrack are deposited over the beach surface and are locally redistributed through wind and wave action, creating a mosaic of bare and wrack-occupied areas (Colombini et al., 2000; Rossi & Underwood, 2002; Jaramillo et al., 2006). This disturbance creates an opportunity for new individuals to become established, determining the taxonomic composition and diversity of species as well as the distribution of invertebrate assemblages as shown in different coastal systems (e.g. Valiela and Reitsma, 1995; Ford et al., 1999; Olabarria et al., 2007; Rodil et al., 2008).

The spatial distribution of wrack debris along the beach profile determines its residence time, since the higher the seaweed is located on the beach, the longer it has presumably been present in the intertidal zone (Colombini and Chelazzi, 2003). Thus, wrack debris accumulates on the upper-shore, where it lies beyond the reach of the wave action, are subjected to drying and ageing processes which could determine the nutritional composition and microclimatic conditions (i.e. temperature and moisture) in wrack deposits (Olabarria et al., 2007; Rodil et al., 2008; MacMillan and Quijón, 2012). Therefore, these habitat features (i.e. biochemical composition of organic matter and microclimatic conditions) could change spatially, in relation to the position of wrack deposits, and temporally as the organic material ages and undergoes the physical dynamics of the beach environment (wind, sand covering, solar exposure, dehydration, etc.) on wrack debris. However, the spatio-temporal changes of habitat features of upper-shore wrack deposits and their relationship with the faunal distribution are poorly understood.

The availability of wrack on sandy beaches is the main factor structuring arthropod communities, mainly beach consumers (Stenton-Dozey and Griffiths, 1983; Dugan et al., 2003; Gonçalves and Marques, 2011). Generally, on sandy shores with high amounts of wrack, arthropods (mainly crustaceans and isopods) tend to concentrate in the supralittoral zone and even become restricted to the driftlines (Gonçalves and Marques, 2011; Bessa et al., 2014). Since many of these organisms form the base of

coastal trophic webs, the availability of wrack to support their biomass is an important factor in the abundance and diversity of marine and terrestrial ecosystems (Polis and Hurd, 1996; Spiller et al., 2010; Mellbrand et al., 2011).

The distribution patterns of arthropods along supralittoral areas may depend on the preference for specific microhabitats and/or food sources that differ according to resource requirements of the different species (Colombini et al., 2000; Pennings et al., 2000; Jaramillo et al., 2006; Colombini et al., 2011). Generally, upper-shore arthropods prefer wrack deposits as previous studies have reported higher abundances and species richness of invertebrates in wrack patches than in bare sand (Dugan et al., 2003; Jaramillo et al., 2006; Ince et al., 2007; MacMillan and Quijón, 2012). This reliance of invertebrates on wrack is generally understood as a response to food availability or refuge against harsh physical conditions (Jaramillo et al., 2006; Olabarria et al., 2007). However, the abiotic factors structuring supralittoral communities as the result from the establishment of wrack deposits have not yet been assessed. Moreover, the position of wrack debris and their relative age play a role in the structure and composition of supralittoral assemblages (e.g. Marsden, 1991; Jaramillo et al., 2006; MacMillan and Quijón, 2012; Ruiz-Delgado et al., 2014), but the habitat features (i.e. microclimatic conditions and nutritional content) of wrack deposits shaping supralittoral arthropods have been little studied.

Consequently, the aim of this study is to evaluate the structuring factors of supralittoral arthropods in relation to the deposition and location of wrack debris. For this, we sampled arthropods in wrack patches and bare sand and measured their habitat features (i.e. microclimatic conditions and nutritional composition of organic matter) at two tidal levels during two contrasting seasons (winter and summer) at two exposed sandy beaches on the south-western coast of Spain. Firstly, we analysed the influence of wrack patches on the structure of assemblages. We hypothesised that at each tidal level: (1) the microclimatic conditions (i.e. temperature and moisture) and labile organic matter (biopolymeric carbon fraction) vary between bare and wrack-occupied areas; (2) density, species richness, and diversity differ between the two microhabitats; and (3) the structure of arthropod assemblages vary between microhabitats, in relation to their habitat features. Secondly, we analysed the influence of the position of wrack deposits on the structure of upper-shore assemblages. In this case, (4) we expected that density, diversity, and structure of arthropod assemblages in wrack patches located at the driftline would differ with respect to patches located above this line, in terms of their

predictable differences in microclimatic conditions and wrack-line ageing. Finally, we predicted that the responses could change spatially, due to local environmental conditions, and seasonally, through the alteration of climate conditions, which could influence the community structure and composition.

MATERIALS AND METHODS

Study area

This study was conducted in two sandy beaches (Levante and Peginas), located on the Atlantic coast of Cadiz (SW Spain) (Fig. 1). This area presents a Mediterranean climate with a wet and mild winter (average precipitation= 83.66 mm and temperature= 13.46ºC for 30 years (1961-1990)) and a dry and warm summer (average precipitation= 7.00 mm and temperature= 24.10ºC for 30 years (1961-1990)). The Gulf of Cadiz is semidiurnal and mesotidal, with a tidal range between 3.2 and 1.1 m (Benavente et al., 2002). The studied beaches have a natural and ungroomed backshore and both of them receive regular allochthonous inputs which are deposited in the supralittoral zone (personal observation). Thus, an estimation of the stranding crop, following methodology of Barreiro et al. (2011), was 35.24 g/m^2 and 10.25 g/m^2 (expressed as average amount of wrack during winter and summer) on Peginas and Levante, respectively. Levante (36°33’37’’N; 6°13’27’’W) located in the outer zone of Cadiz Bay, is a dune-backed and dissipative beach. It is wide beach (width approximately 100 m) characterized by fine sands (mean grain size = 0.18 mm; Wentworth scale (1922)) and gentle slope (2.09%; Emery’s profiling technique (1961)). Peginas (36°39’43’’N; 6°24’15’’W) located at north of the Cadiz Bay, is an intermediate beach, backed by low cliffs and faced by rocky shore platform. It is a narrow beach (width approximately 50 m), with medium sands (mean grain size = 0.35 mm) and a steep slope (6.50%). The driftlines occupied approximately 3% and 9% of the entire intertidal of Peginas and Levante, respectively. Wrack deposits collected at Levante were composed of two seagrass species: *Cymodocea nodosa* and *Zostera noltii*. Meanwhile at Peginas the deposits were a mixture of red and brown macroalgae: *Halopithys incurva*, *Jania* sp., *Cladostephus spongiosus* and *Halopteris scoparia*.

Figure 1. Location of the 2 exposed sandy beaches (Peginas and Levante) on the south-western coast of Spain

Sampling methods and laboratory analysis

Upper-shore invertebrates from wrack and bare sand were collected at Levante and Peginas beaches during both wet (winter, January to March) and dry (summer, June to September) seasons of the year 2011. Thus, each season comprised three temporal replicates. In this study, the samples were collected at two tidal levels, namely the level at which wracks are stranded during the last highest spring tide and located above the current high tide line and another one at which wracks are deposited during the last high tide and located at the current driftline (hereafter upper and lower level, respectively).

The sampling points were randomly designated along each tidal level in covered and uncovered wrack areas during low spring tides. The along-shore distance of the sampling area was 50 m, while the across-shore distance was 5 m above and below wrack bands. In this study, "band" is defined as the wrack-covered line parallel to the tide line. For each tidal level and sampling date, 6 random samples were collected in each microhabitat (i.e. wrack patches and bare sand) with a total of 72 samples per habitat and tidal level (N=144 per site). Wrack-associated fauna and burrowing fauna underneath the wrack patches were collected in wrack covered areas. To do this, algal wrack at the surface and 20 cm of sediment were taken with a 15-cm diameter core. Moreover, samples were taken in the nearby bare sand, with the same core which penetrated also 20 cm in depth, to measure the abundance of invertebrates in areas not covered by wrack. At the free end of the corer, a plastic bag was used to prevent mobile fauna (mainly insects and amphipods) from escaping. All samples were preserved in

70% ethanol. Temperature (°C) and moisture (%) were measured *in situ* underneath wrack patches and in the bare sand (n=3) in the first 5 cm of depth, at each tidal level and sampling date. For temperature measurement, a manual thermometer was used and a TDR (Time Domain Reflectometry) was used for moisture, expressed as volumetric water content. Moreover, subsamples of wrack (±5g) and bare sediment (±10g) for estimation of the amount of labile organic matter in each microhabitat were collected (n=3) and frozen (-20 °C) until analysed.

In the laboratory, samples were sieved through a 0.5 mm mesh and the retained invertebrates were sorted and identified to the lowest possible taxonomic level. The total organic matter (OM) of wrack and sediment was measured as the difference in weight of the dried samples (60ºC to a constant weight) before and after ignition in a muffle furnace at 450°C for 5 h. Moreover, biopolymeric carbon fraction (BPC) was reported as an estimate of the labile fraction available to consumers (Fichez, 1991) and was calculated as the sum of the main biochemical classes (carbohydrates, proteins and lipids), as previous studies had reported for beach sediment (Cividanes et al., 2002; Incera et al., 2003) and wrack patches (Rodil et al., 2008). Total carbohydrates (Dubois et al., 1956), proteins (Markwell et al., 1978), and lipids (Bligh and Dyer, 1959; Marsh and Weinstein, 1966) were analysed and measured as $\mu g.gdw^{-1}$ of the sediment and the wrack patches. Moreover, protein to carbohydrate ratio (PRT:CHO) was calculated to estimate the age of organic matter of wrack deposited at each tidal level. This ratio has been used in previous studies to estimate the age of organic matter of beach sediments (e.g. Cividanes et al., 2002; Incera et al., 2003).

Data analysis

Differences in abiotic (microclimatic conditions and food availability) and biotic (total density, species richness and diversity (Shannon-Wiener index)) data were tested by a permutational analysis of variance (PERMANOVA; Anderson, 2001) based on a five-factor design: Habitat (Ha) with 2 levels: wrack and bare sand; Tidal Level (Le), with 2 levels: upper and lower; Beach (Be), with 2 levels: Peginas and Levante; and Season (Se) with 2 levels: winter and summer as fixed factors; and Date (Da) with 6 levels (3 sampling events in each season) as random factor and nested within each season. A four-way PERMANOVA was run to analyse differences in the nutritional composition between wrack deposited at each tidal level, beaches, seasons, and sampling date nested in each season. Euclidean distance matrices were used based on

9999 permutations of residuals under a reduced model. Data were fourth root transformed prior to analysis. The homogeneity of dispersion was checked using PERMDISP based on deviations for medians (Anderson et al., 2008). Statistically significant effects ($p<0.05$) were analysed by a posteriori pair-wise comparisons to discriminate differences among the interaction term or the levels of the main factors (Anderson et al., 2008).

For the analysis of the arthropod community, a five-way permutational multivariate ANOVA (PERMANOVA; Anderson, 2001) was applied using the same design as in the univariate analysis. Only significant interaction term (Habitat×Level) ($p<0.05$) were further investigated through a series of *a posteriori* pair-wise comparisons for each beach and/or season. Prior to pairwise tests, permutational test of multivariate dispersion (PERMDISP; Anderson, 2006) was employed to investigate dispersion effects on this interaction term. When two (or more) factors are crossed with one another, it is easily possible to confuse a dispersion effect with an interaction effect (Anderson, 2008). When PERMDISP analysis was significant, patterns in ordination plots and the relative sizes of within and between-group resemblances (i.e. pairwise test Habitat×Level) were examined to ensure that, in addition to the dispersion effect, a location effect occurred (Anderson, 2008). Based on fourth root transformed species abundance, data similarities were calculated using the Bray–Curtis coefficient. The statistical significance of variance components was tested using 9999 permutations and was set at a threshold of 0.05. When found significant differences in the PERMANOVA tests, the similarity percentage routine (SIMPER) was used to identify which taxa contributed the most to the dissimilarities (Clarke and Warwick, 1994).

A BIO-ENV analysis was applied to explore the degree to which the chosen environmental variables explain the arthropod assemblage structures (Clarke and Warwick, 1994). For this, biotic and abiotic matrices were constructed using the Bray–Curtis dissimilarity index (based on square-root transformed data) and Euclidean distances, respectively. The relationship between the individual density of wrack-associated species and the habitat features (microclimatic conditions and nutritional composition) of wrack patches was estimated by the Spearman's rank correlation coefficient (ρ). All analyses were performed using Primer v.6 and PERMANOVA (PRIMER-E Ltd., Plymouth, UK).

RESULTS

Microclimatic conditions and food availability and composition in wrack patches and bare-sand areas

Temperature and moisture varied significantly between habitats (i.e. wrack patches and bare sand), but these differences were not consistent between levels, beaches and seasons (i.e. significant Habitat×Level×Beach×Date (Season) interaction; Table S1). Temperature was significantly lower in wrack patches than bare sand, specially at lower levels during winter (Table S2; Fig. 2a), while moisture was higher in wrack patches than in bare sand, especially at the upper level during summer (Table S2; Fig. 2b). Moreover, temperature in wrack patches was higher in the upper than in the lower band on both beaches during winter and only on Levante during summer (Table S2; Fig. 2a). Moisture showed the opposite pattern (i.e. higher in the lower than in upper band), and this variation was consistent between seasons and beaches (Table S2; Fig. 2b).

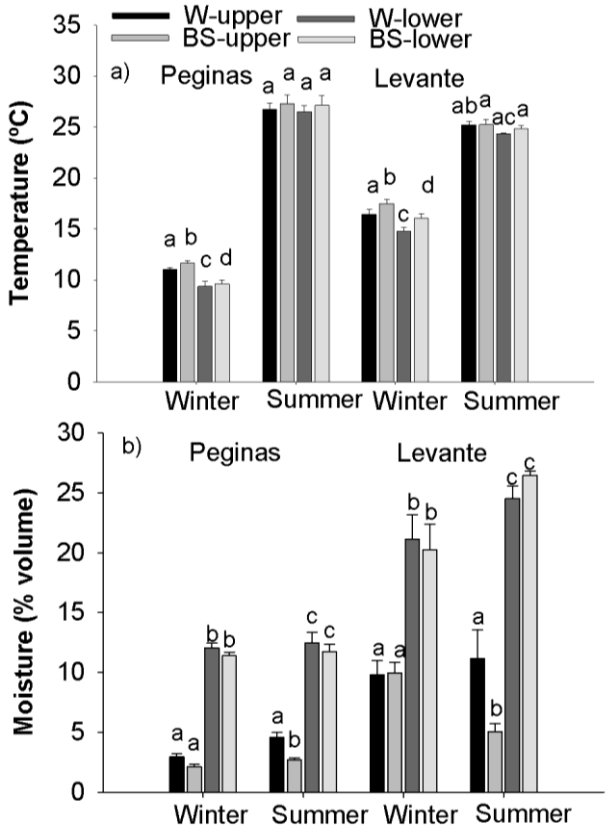

Figure 2. Mean (±SE; n=18 average 3 dates) of a) temperature and (b) moisture in the wrack patches (W) and in the bare sand (BS) on the upper and on the lower level at both beaches (Peginas and Levante) and in both seasons (winter and summer). Different letters represent significant differences and same letters represent no significant differences.

On the other hand, OM and BPC concentration, as a measure of the organic matter availability and the food quality for consumers, differed between habitats, across levels, beaches and seasons (i.e. significant Habitat×Level×Beach×Date (Season) interaction, Table S1). Both variables were higher in wrack patches than in bare sand, as might be expected, and this pattern was consistent across tidal levels, beaches and over seasons (Table S2). Moreover, the total OM was greater in wrack patches deposited on the upper than on the lower level (Fig. 3a; Table S2), except at Peginas beach during summer. However the labile organic matter (BPC), was higher in wrack patches of the lower than the upper level during winter, but this difference was only significant at Levante beach, while the opposite pattern was detected during summer at both beaches (Fig. 3b; Table S2).

On the other hand, the nutritional composition of the wrack patches varied between tidal levels, although this pattern was no consistent across beaches and seasons (i.e. significant Level×Beach×Date (Season) interaction, Table S3). The carbohydrate concentration was higher in wrack patches of the upper than the lower level during both seasons at Peginas (Fig. 3c; Table S4), while the opposite pattern was observed at Levante beach during winter (Fig. 3c). Moreover, proteins were also more concentrated in wrack patches at the upper than at the lower level during summer at both beaches (Table S4), and conversely, during winter (Fig. 3d). As a result, the ratio PRT:CHO differed between wrack bands, but this pattern was no consistent between seasons (significant Level×Date (Season) interaction; Table S3). During winter, the ratio PRT:CHO was higher in wrack patches at the lower than at the upper level, and, conversely, during summer (Fig. 3f; Table S4). Lipids were more concentrated in wrack patches of the upper than the lower level at both seasons, but this difference was only significant at Peginas beach (Fig. 3d; Table S4).

Composition and univariate measures for supralittoral arthropods

A total number of 881 individuals belonging to 36 species were collected in wrack patches, while 56 individuals belonging to 7 species were found in the bare sand at both beaches (Table S5). Species collected in the bare sand were the same that those found in wrack patches, but they presented higher abundances in wrack patches than in the nearby bare sediment. Moreover, wrack patches attracted several species that not were found in bare sands (Table S5). At Levante, wrack patches were dominated by the amphipod *Talitrus saltator* (47%), adults of *Phaleria bimaculata* (12%), Tenebrionidae

larvae (17%), individuals from the family Hydrophilidae (8%) and the staphylinid *Carpelimus rivularis* (6%). On the other hand, *Talitrus saltator* (20%), adults of *Phaleria bimaculata* (14%), the staphylinids *Cafius xantholoma* (7%) and *Remus sericeus* (7%) and the Tenebrionidae larvae (6%) were the most representative taxa of wrack patches at Peginas beach. In terms of frequency, the amphipod *Talitrus saltator*, adults of *Phaleria bimaculata* and Tenebrionidae larvae were constant taxa throughout the study period.

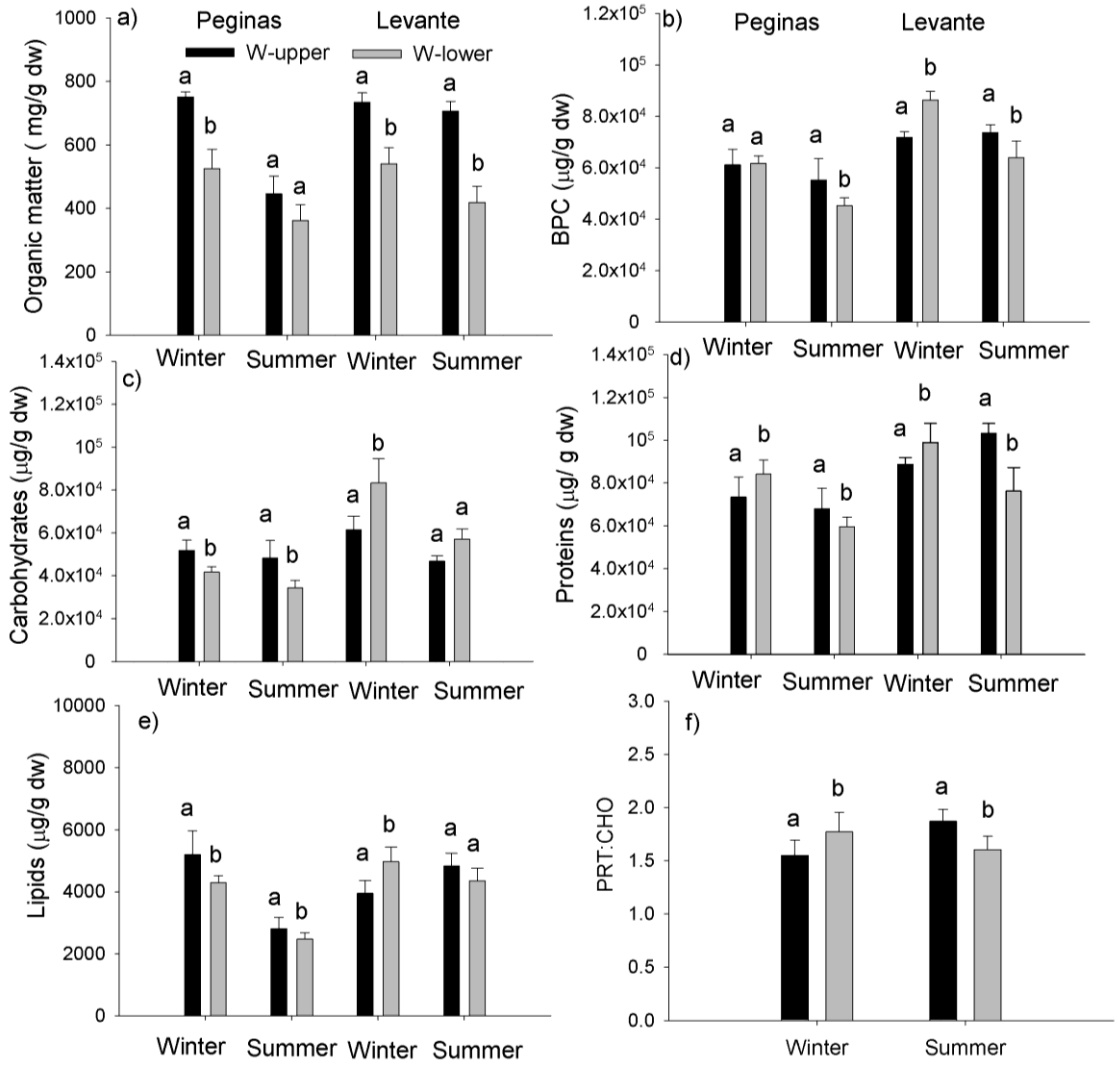

Figure 3. Mean (±SE; n=18 average 3 dates) of a) total organic matter (OM), b) biopolymeric carbon fraction (BPC), c) carbohydrate, d) protein, and e) lipid concentrations in the wrack patches on the upper and on the lower level at both beaches (Peginas and Levante) and in both seasons (winter and summer); f) protein to carbohydrate ratio in the wrack patches (W) on the upper and on the lower level in both seasons (winter and summer). Different letters represent significant differences and same letters represent no significant differences.

Total density and diversity varied significantly between habitats, but there was no consistency between beaches, tidal levels and seasons (i.e. Habitat×Level×Beach×Season interaction; Table S6). Fauna was more abundant and diverse in the wrack patches than in the bare sand at each tidal level in both seasons and on both beaches (p (MC) < 0.05 for HaxLe interaction within beach and season; Fig. 4a, c). Moreover, total density and diversity in wrack patches and bare sand not varied between tidal levels (p (MC) > 0.05 for HaxLe interaction within beach and season), except in wrack deposits at Peginas during winter (p (MC) >0.05). Species richness differed also between the two habitats, but this pattern was not consistent between beaches and seasons (i.e. Habitat×Beach×Season interaction, Table S6). Pairwise comparisions showed that the number of species was significant higher in wrack patches than in bare sand on both beaches during both seasons (p (MC) < 0.05 for all terms of the interaction; Fig. 4b), but the magnitude of the differences was higher on summer (p (MC) = 0.005 at Peginas and p (MC) = 0.001 at Levante) than on winter (p (MC) = 0.02 at Peginas and Levante).

Analysis of arthropod assemblages in wrack patches and bare sand

Arthropod assemblages differed between microhabitats but these differences were inconsistent between beaches, levels and seasons (i.e. significant Habitat×Level×Beach×Date (Season) and Habitat×Level×Season interactions, Table S6). Pair-wise comparisons showed that arthropod assemblages differed between the two habitats at each tidal level, but only during summer (pairwise comparisons Table S7). Notwithstanding the small-scale temporal variability within this season, the dissimilarity of assemblages among habitats was greater on Levante (49%) than on Peginas beach (30%). According to the results of SIMPER analysis, the responsibility for the differences between wrack patches and bare sand during summer was shared by *Talitrus saltator*, *Phaleria bimaculata*, Tenebrionidae larvae, and Staphylinidae species (Table 1) which were among the dominant species of wrack patches but very scarce in bare sand (Table S5). Thus, in this season a clear community structure was detected between the two microhabitats on both beaches.

On the other hand, pair-wise test showed that arthropod assemblages inhabiting wrack patches differed between tidal levels, especially during summer at Levante beach (Table S7), but did not differ in bare sand at both beaches. Focusing on the distribution pattern of the main species in the wrack deposits, we found that the density of *T.*

saltator varied between tidal levels and these variations were not consistent between beaches (i.e. significant Level×Beach×Date (Season) interaction; Table S8).

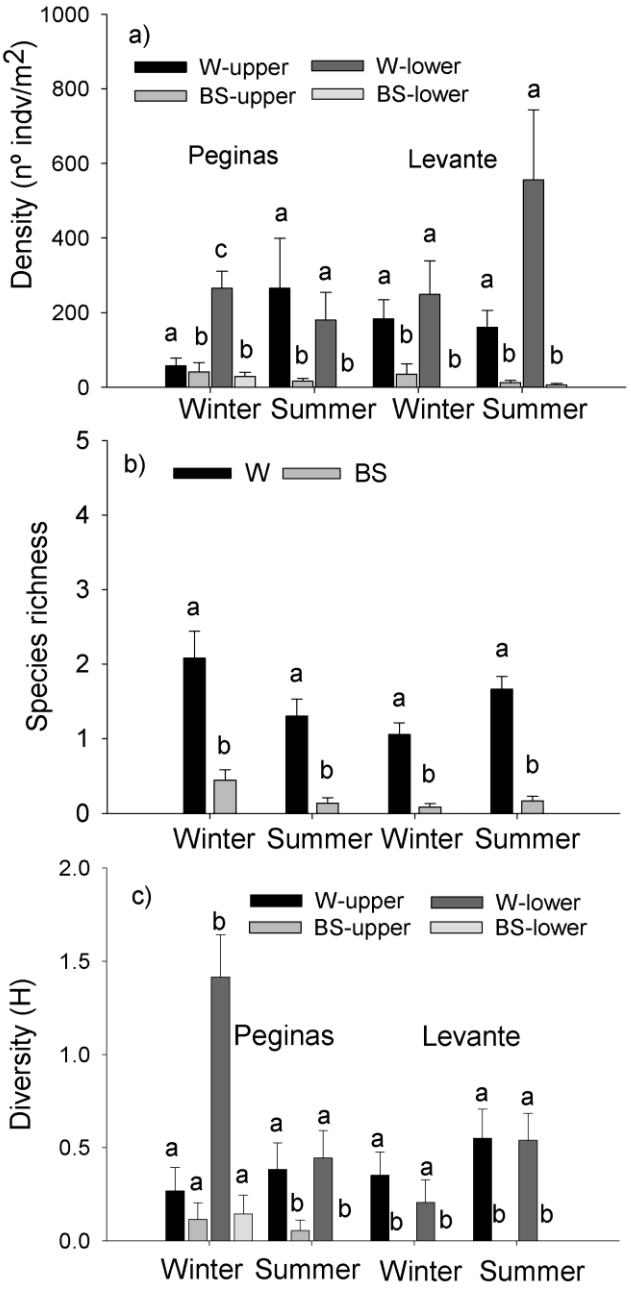

Figure 4.Mean (±SE; n=18 averaged 3 dates) of a) density (nº indv/m^2) in the wrack patches (W) and in the bare sand (BS) on the upper and on the lower level and b) species richness averaged in the wrack patches (W) and in the bare sand (BS) at both beaches (Peginas and Levante) and seasons (winter and summer); c) diversity (Shannon-Wiener index) averaged in the wrack patches (W) and in the bare sand (BS) on upper and lower level at both beaches (Peginas and Levante). Different letters represent significant differences and same letters represent no significant differences.

The posterior pairwise comparisons for this significant interaction term showed that *T. saltator* was more abundant in wrack patches of lower level than in those of upper level, but was only significant at Levante beach (pairwise test p (MC) <0.01; Fig. 5a). The density of adults of *P. bimaculata* did not show significant differences among wrack bands and this pattern was consistent between beaches (i.e. no significant interactions; Table S8). However, this species appeared mainly in the upper band of both beaches during summer (Fig. 5b). Tenebrionidae larvae showed pattern similar to that of adults of the same family, varying between wrack bands, but inconsistently between beaches (i.e. significant Level×Beach, interaction; Table S8). Tenebrionidae larval density was higher in the wrack patches of the upper level than in those of the lower level, but was significant only at Levante beach (pairwise test p (MC) <0.001; Fig. 5c). Moreover, Sthaphylinid species such as *C. rivularis* was found only at Levante, while *C. xantholoma* and *R. sericeus* were found at Peginas and all of them were caught mostly in the wrack patches deposited along the lower level (Fig. 5d).

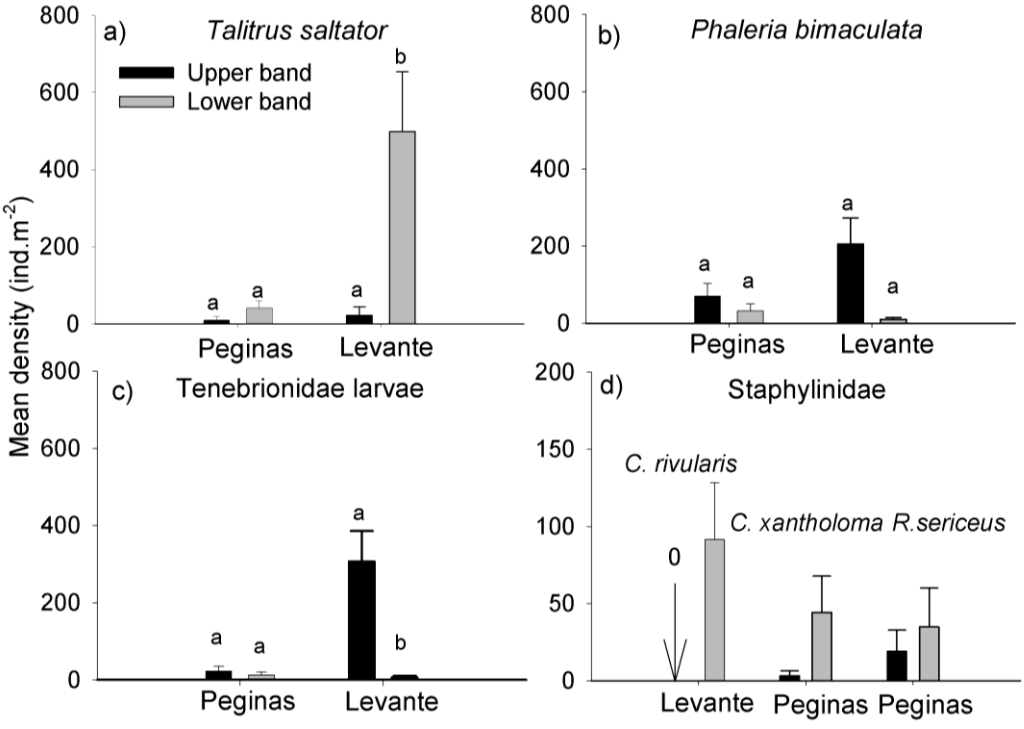

Figure 5.Mean (±SE; n=18 average 3 dates) of density of a) *T. saltator*, b) *P. bimaculata* c) Tenebrionidae larvae, d) Staphylinid species in the wrack patches on the upper and on the lower level at each beach (Levante and Peginas) during summer. Different letters represent significant differences and same letters represent no significant differences. No ANOVAs were conducted for Staphylinid species.

Table 1 Taxa identified as important in characterizing and separating habitats (wrack patches and bare sand) according to the similarity and dissimilarity values obtained by SIMPER analysis for summer.

Similarities (>10%)				Dissimilarities (>5%)			
Summer	**Peginas**		**Levante**	**Summer**	**Peginas**		**Levante**
Taxa	Contrib (%)	Taxa	Contrib (%)	Taxa	Contrib (%)	Taxa	Contrib (%)
	Bare sand		**Bare sand**		**BS vs W**		**BS vs W**
Diptera larvae	77.78	*T. saltator*	100	*P. bimaculata*	28.31	*T. saltator*	31.41
Tenebrionidae larvae	22.22			Tenebrionidae larvae	19.13	Tenebrionidae larvae	26.17
	Wrack		**Wrack**	*T. saltator*	13.98	*P.bimaculata*	17.28
P. bimaculata	44.41	Tenebrionidae larvae	36.46	*R. sericeus*	10.63	Hydrophilidae sp.	12.72
Tenebrionidae larvae	18.59	*T. saltator*	30.09	Diptera larvae	10.59	*C. rivularis*	5.84
T. saltator	14.02	*P. bimaculata*	15.15	*C. xantholoma*	9.32		
R. sericeus	8.19	Hydrophilidae sp.	13.93				
C. xantholoma	8.15						

Relationship between arthropod assemblages and habitat features

The results of the BIO-ENV analyses (Table 2) showed that, during summer, the BPC concentration alone best explained the pattern of arthropod assemblages between wrack patches and nearby bare sand both at Peginas ($\rho s = 0.591$; $p<0.01$) and Levante beach ($\rho s = 0.425$; $p<0.05$). BPC combined with temperature or moisture showed similar results at both beaches, but reached lower levels of correlation than the BPC alone (Table 2).

Table 2 Results of the BIO-ENV analysis (resumed to the best parameter alone and the best combination of parameters) for environmental variables (moisture, temperature and BPC) and arthropod assemblages of both habitats (bare sand (BS) and wrack patches (W)) during summer. Spearman's rank correlation coefficients (ρw) are showed.

Habitat	Peginas				Levante			
	Parameter	ρw	Combination	ρw	Parameter	ρw	Combination	ρw
BS and W	**BPC**	**0.591**	Mois+BPC	0.357	**BPC**	**0.425**	Temp+BPC	0.298
			Temp+BPC	0.328			Mois+BPC	0.291
			Temp+Mois+BPC	0.235			Temp+Mois+BPC	0.190

Bold indicates best combination overall

Table 3 Correlation analyses between abundance of the dominant species and habitat features (microclimatic conditions (temperature (Tª) and moisture) and nutritional composition (total carbohydrates (Car), proteins (Prot) and lipids (Lip)) of wrack patches. Spearman's rank correlation coefficients are presented for the summer data (n=18).

Sites	**Species**	Tª	Moisture	Car	Prot	Lip
Peginas	*T. saltator*	0.091	0.443*	0.091	0.318	0.250
	P. bimaculata	0.264	0.466*	-0.275	0.442*	-0.251
	Tenebrionidae larvae	0.465*	0.077	0.155	0.077	0.103
Levante	*T. saltator*	0.210	0.407•	0.428•	0.033	0.209
	P. bimaculata	0.066	0.736**	0.560*	0.077	0.033
	Tenebrionidae larvae	0.205	0.771**	0.568*	0.118	0.118

***p<0.001; **p<0.01;*p< 0.05; •0.05< p<0.06

Moreover, the relationship between density of the main species inhabiting wrack patches and abiotic variables was explored (Table 3). In this way, we found that *T.*

saltator density in wrack patches was positively correlated with moisture on both beaches and also with the carbohydrate concentration at Levante beach. Moreover, P. bimaculata density was negatively correlated with moisture and protein or carbohydrate concentration at Peginas and Levante, respectively. Similar relationships were found for Tenebrionidae larvae, being negatively correlated with temperature, moisture, and carbohydrate concentration at Peginas and Levante beach, respectively. No relationship was detected between staphylinid species (*C. rivularis*, *R. sericeus* and *C. xantholoma*) and the abiotic variables measured.

DISCUSSION

Distribution pattern of supralittoral arthropods: wrack deposits vs. bare sand

Allochthonous inputs have been defined as the main factor driving distributional patterns of beach invertebrate assemblages (Griffiths and Stenton-Dozey, 1981; Jędrzejczak, 2002b; Jaramillo et al., 2006; MacMillan and Quijón, 2012). Our results support this notion for density, number of species, and diversity of supralittoral arthropods, which were significantly higher in wrack patches than in nearby bare areas at both tidal levels. According to the results for bare-sand samples, the density and number of species in the supralittoral zone of the two beaches studied would be much lower if the wrack patches were absent. Therefore, wrack deposits enhance the abundance and species richness of the upper-shore arthropods. Studies such as Defeo et al. (1992), Dexter (1992), Jaramillo and McLachlan (1993), Brazeiro and Defeo (1996), Veloso et al. (2003) and Rodil et al. (2006) have analysed community structure, at different levels, and in terms of zonation patterns, focusing attention on the intertidal macrofauna. However, little relevance has been given to terrestrial arthropods (e.g. dipterans, coleopterans, isopods, amphipods), although it has been demonstrated that they have an important place in the composition of the whole macrofauna community as well as in their structure, especially in the supralittoral zone, where its relative importance in the community composition increases (de la Huz and Lastra, 2008; Gonçalves et al., 2009).

Once stranded on the beach, algal wracks can create a new habitat with different microclimatic characteristics than the surrounding areas (Colombini and Chelazzi, 2003) and provide organic matter to poorly productive sandy beaches (McLachlan and Brown, 2006). This process increases the spatial heterogeneity and in turn the

environmental range available for organisms on the beach. Our results demonstrated that wrack patches create a habitat with microclimatic conditions and food availability which attract more diverse fauna than the nearby bare sand (see above), and determine the composition and structure of supralittoral assemblages. Generally, upper shores arthropods exhibited habitat selection, preferring wrack patches over bare sand (Dugan et al., 2003; Jaramillo et al., 2006; Ince et al., 2007; MacMillan and Quijón, 2012), although this pattern was detected only during summer. In fact, previous studies have pointed out that wrack-associated fauna vary seasonally, due to the influence of the climate conditions on the numbers of colonists in each season, the summer the season with having the highest abundance of macrofauna (Behbehani and Croker 1982; Gonçalves and Marques, 2011; Dufour et al., 2012). During this season, the composition and structure of arthropod assemblages differed between microhabitats on both beaches; in this way, several species were associated with wrack debris, but no species were encountered only on sand devoid of wrack. The major components of the wrack-associated fauna were talitrid amphipods, tenebrionids, staphylinids and dipterans. This is similar to what has been observed on other beaches of the world (Behbehani and Croker, 1982; Inglis, 1989; Colombini et al., 2002; Jaramillo et al., 2006; Olabarria et al., 2007). *T. saltator*, *P. bimaculata*, Tenebrionidae larvae, and Staphylinidae were the taxa that most contributed to the dissimilarity between the two microhabitats during summer at both beaches. These species were more abundant in wrack patches (either on upper or lower band) than bare sand, where these were practically absent (e.g. tenebrionids and staphylinids species) or present very low abundances (e.g. talitrids). In fact, previous studies have demonstrated that talitrid amphipods as well as tenebrionid and staphylinid beetles show an association with wrack deposits (Colombini et al., 1998, 2000; Jędrzejczak, 2002b; Dugan et al., 2003; Jaramillo et al., 2006; MacMillan and Quijón, 2012). However, species composition differed between beaches, which might be explained by different local environmental conditions (shoreline type, grain size, wrack composition, etc.). At Peginas the presence of vegetated low cliffs could favour dipteran species dispersion to the beach, where larvae and adults could use wrack deposits as a food and as a hospitable environment for reproduction and growth (Lavoie, 1985; Inglis, 1989; Jędrzejczak, 2002b). Moreover, beaches also differed in the presence of Staphylinidae species (e.g. *C. rivularis* was found on Levante beach, while *C. xantholoma* and *R. sericeus* and larvae were found on Peginas) and the presence of Hydrophilidae species, found only at

Levante beach. Despite small differences in species composition between beaches, this study demonstrates that wrack deposits can attract species that typically not occur in bare beach sands, enhancing diversity, or increasing abundance of supralittoral fauna.

Several studies have reported that wrack deposits provide the main food source for supralittoral macrofauna (Colombini et al., 2000; Adin and Riera 2003; Ince et al., 2007; Poore and Gallagher, 2013). Consistent with this, we found that the BPC concentration, as estimate of the potential food for consumers, was higher in wrack patches than in bare sand and this variable could explain the association of supralittoral arthropods with wrack patches. In fact, previous studies demonstrated that some terrestrial arthropods such as *T. saltator* or species of the genus *Phaleria* feed on organic matter of stranded algae (Adin and Riera 2003; Ince et al., 2007; Lastra et al., 2008; Colombini et al., 2011), although the use of wrack as a food resource depends on several factors, such as amount, composition, nutritional quality, and state of decomposition of wrack deposits (Ince et al., 2007; Colombini et al., 2009). This study highlights the labile organic matter as factor structuring of upper-shore community, mainly beach consumers. Moreover, wrack deposits could be used as refuge from environmental conditions (e.g. Inglis, 1989; Colombini et al., 2000). Results indicated that temperature or moisture, combined with BPC, also explained the distribution pattern of arthropods during summer, in which moisture and temperature measured in wrack patches were higher or lower than in nearby bare sand, respectively, at both beaches. In this way, wrack deposits could enable arthropods to cope with harsh climatic conditions (i.e. high air temperature and low humidity) during summer, avoiding dehydration and thermal stress by staying inside or underneath of wrack patches. Thus, in this season a clear structural pattern of assemblages was found between wrack deposits and bare sand. Therefore, wrack deposits seem to offer more hospitable conditions than bare sand, considering microclimatic factors and food availability, which drive the association of supralittoral arthropods with wrack debris.

The habitat features of wrack deposits and their influence in arthropod assemblages

The position of wrack deposits over the beach surface, and, therefore their relative ageing, could influences the microclimatic conditions and biochemical composition of stranded algae (Colombini and Chelazzi, 2003; Jaramillo et al., 2006; Rodil et al., 2008). This study demonstrated that upper wrack deposits were characterized by high temperature, low moisture and a low protein to carbohydrate ratio, while lower wracks

presented the opposite features, because the former tend to remain longer on the beach than those deposited at the high tide line (lower band), which could lead to their dehydration and ageing (Orr et al., 2005; Jaramillo et al., 2006). Both processes contribute to the decomposition of the algal tissue and its loss of organic matter (Ochieng and Erftemeijer, 1999; Jędrzejczak, 2002a; Rodil et al., 2008), ultimately altering the nutritional composition of the wrack, as our results showed (see above). However, in our study, the chemical composition of wrack bands changed seasonally, probably due to the influence of environmental conditions on the physical fragmentation and biological (bacteria, fungi, meiofauna, detritivores, etc.) degradation (Jędrzejczak, 2002b), which could hinder the appearance of a clear pattern of variation between wrack bands.

An effect of wrack bands on the structure of assemblages was detected, but not on the biological attributes of the communities. The role of wrack deposits shaping supralittoral arthropods has recently been demonstrated for different types of wrack deposits (Ruiz-Delgado et al., 2014). This result contrasts with the results of Ince et al. (2007), who found no differences in the abundance of coleopterans and talitrid amphipods between upper and lower zones delimited on the upper shores of Australian sandy beaches. Nevertheless, in that study no abiotic variables of wrack deposits were measured to explain the pattern of abundance of upper-shore arthropods. The utilization of wrack deposits by arthropods can vary temporally and spatially (e.g. Gonçalves and Marques, 2011, MacMillan and Quijón, 2012). Our results demonstrated that the effect of wrack bands on the structure of assemblages was clearer during summer than winter, when the highest numbers of colonizers were found at both beaches studied (see above). Moreover, this pattern was clearer at Levante than Peginas beach. This could be related with the major abundance of three dominant taxa (*T. saltator*, *P. bimaculata*, Tenebrionidae larvae) at Levante than Peginas. Different local environmental conditions (grain size, wrack composition, shoreline type, etc.) at the two beaches, could influence on the species density (e.g. Gonçalves et al., 2009). Therefore, the local availability of invertebrates was probably a critical factor in order to explain temporal and spatial differences in wrack utilization (e.g. MacMillan and Quijón, 2012).

Changes of habitat features in relation to the ageing of wrack debris could play an undeniable role in the utilization of wrack by the arthropods (e.g. Jaramillo et al., 2006; Rodil et al., 2008; MacMillan and Quijón, 2012). Different degree of dehydration and ageing of wrack debris can offer different microclimatic conditions and food

quality, which lead to distribution of several arthropod species in relation to their physiological tolerances (Lavoie, 1985) locomotory activity (e.g. Colombini et al., 1998; Fallaci et al., 1999) and/or their preference for wrack with different stages of ageing (Pennings et al., 2000; Colombini and Chelazzi, 2003). In this way, species showed segregation between wrack bands in relation to the availability moisture and/or the nutritional content of wrack debris at both beaches. For instance, the amphipod *T. saltator* was more abundant in wrack deposited at the lower than at the upper level, and its abundance was positively correlated with moisture in wrack debris. This result is consistent with previous studies that have reported closer association of talitrid amphipods with new and fresh algal wrack deposits (Marsden, 1991; Jędrzejczak, 2002b; Jaramillo et al., 2006; Ruiz-Delgado et al., 2014). Therefore, it is possible that the individuals may select wrack patches initially based on their risk of desiccation stress (Marden, 1991), but also as food source (Adin and Riera, 2003; Olabarria et al., 2009). However, no relationship was detected between *T. saltator* density and the nutritional composition of algae tissue, since food value alone does not determine habitat preferences by talitrid amphipods (Poore and Gallagher, 2013). Other tissue traits such as toughness, the amount of chemical defenses and palatability, could determine the selectivity of talitrid amphipods for algae as food source (Pennings et al., 2000; Rothäusler et al., 2006; Duarte et al., 2010; 2014) and therefore, their distributional pattern in wrack deposits. On the other hand, *P. bimaculata* and Tenebrionidae larvae dominated the wrack patches deposited on the upper levels at both beaches, and their abundances were negatively correlated with moisture and proteins or carbohydrate contents. This result might be related to their preference for aged and dry wrack deposits as well as for lower moisture contents in the sand as reported for different species of the genus *Phaleria* (Aloia et al., 1999; Colombini et al., 2002; Jaramillo et al., 2006). In fact, Colombini et al. (2011) reported adults and larvae of different species of genus *Phaleria* feeding on marine debris and terrestrial plants, which could explain that both of them were found mainly on the upper level of the beaches. By contrast, Staphylinidae species are very sensitive to dehydration (Colombini et al., 1998; Garrido et al., 2008), so that could account for the fact that staphylinids were found mostly in wrack deposited along the lower bands, which were composed of wet wrack patches. However, we found no significant relation with the moisture in wrack deposits. The presence of staphylinid beetles in wrack deposited at the lower band could be explained by the presence of larvae of dipterans and/or

amphipods in wrack patches, which attracted predators such as *C. xantholoma* and *R. sericeus*, as previous studies have demonstrated for others staphylinid species (Colombini et al., 2000; Ince et al., 2007). This could explain the lack of a significant correlation with any of the variables measured.

From the results, we conclude that stranded wrack deposits create a new habitat with different microclimatic characteristics and food availability than the nearby bare sand, which structure diversity and composition of supralittoral arthropods. Moreover, the results suggest that the distribution of wrack deposits in bands entails changes in their habitat features which influence on the distributional pattern of arthropod assemblages. This study stressing the importance of the habitat heterogeneity to maintain abundant and diverse communities on exposed sandy beaches. However, manipulative experiment to evaluate the biological interactions and the feeding strategies are needed to understand the distributional patterns of arthropod assemblages.

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SUPLEMENTARY MATERIAL

Table S1 Results of PERMANOVA analysis performed for temperature, moisture, total organic matter (OM), and biopolymeric carbon fraction (BPC).

		Temperature		Moisture		O.M		BPC	
Source	**df**	**MS**	**PseudoF**	**MS**	**PseudoF**	**MS**	**PseudoF**	**MS**	**PseudoF**
Habitat (Ha)	1	0.012	3.26	0.167	5.26	99.314	4047.60***	1745.80	18973.00***
Level (Le)	1	0.050	53.94**	9.882	150.03**	0.268	7.99*	1.637	9.67*
Beach (Be)	1	0.257	33.52**	4.386	53.55**	0.027	0.44	5.132	25.52**
Season (Se)	1	4.563	201.69***	0.022	0.15	0.020	0.36	0.963	1.99
Date (Da(Se))	4	0.023	100.02***	0.150	25.29***	0.057	3.17*	0.484	21.63***
HaxLe	1	0.000	0.02	0.128	3.54	1.056	9.86*	1.895	19.20*
HaxBe	1	0.000	0.06	0.009	0.49	0.261	7.96*	0.158	0.60
HaxSe	1	0.003	0.87	0.038	1.21	1.209	49.27**	0.034	0.37
LexBe	1	0.001	1.07	0.022	0.14	0.042	0.36	0.258	1.44
LexSe	1	0.028	30.98**	0.079	1.20	0.001	0.04	0.003	0.02
BexSe	1	0.583	76.11***	0.053	0.65	0.165	2.63	0.884	4.40
HaxDa(Se)	4	0.004	16.64***	0.032	5.34***	0.025	1.37	0.092	4.11**
LexDa(Se)	4	0.001	4.07**	0.066	11.09***	0.033	1.86	0.169	7.56***
BexDa(Se)	4	0.008	33.85	0.082	13.79***	0.063	3.49**	0.201	8.98***
HaxLexBe	1	0.000	0.11	0.000	0.00	0.007	0.16	0.412	1.51
HaxLexSe	1	0.000	0.04	0.092	2.55	0.001	0.01	0.728	7.37*
HaxBexSe	1	0.001	0.23	0.006	0.34	0.051	1.57	1.410	5.31
LexBexSe	1	0.005	3.29	0.356	2.23	0.013	0.11	0.018	0.10
HaxBaxDa(Se)	4	0.003	13.76***	0.036	6.09***	0.107	5.95**	0.099	4.41**
HaxBexDa(Se)	4	0.005	20.18***	0.018	3.09*	0.033	1.82	0.266	11.87***
LexBexDa(Se)	4	0.001	6.14***	0.160	26.87***	0.118	6.57***	0.180	8.04***
HaxLexBexSe	1	0.000	0.01	0.036	1.51	0.108	2.67	0.017	0.06
HaxLexBexDa(Se)	4	0.004	19.08***	0.024	4.00**	0.040	2.25*	0.272	12.17***
Residual	96	0.000		0.006		0.018		0.022	
Total	143								
Transformation		4th root		4th root		4th root		log (x+1)	

***p<0.001;**p<0.01;*p<0.05; n.s=not signicant

Table S2 Results of the pair-wise comparisons of the PERMANOVA analysis performed to compare moisture, temperature, biopolymeric carbon fraction (BPC) and organic matter between bare sand (BS) and wrack patches (W) at each tidal level (upper (UB) and lower (LB)) within each season and beach (Levante and Peginas).

Moisture		Wrack vs Bare sand				Upper vs Lower band	
		Levante		Peginas		Levante	Peginas
Season	Date	Upper	Lower	Upper	Lower	W	W
Winter	M1	n.s	n.s	W>BS*	n.s	LB>UB*	LB>UB***
	M2	n.s	n.s	n.s	n.s	n.s	LB>UB***
	M3	n.s	n.s	n.s	n.s	LB>UB***	LB>UB***
Summer	M1	W>BS***	n.s	n.s	n.s	LB>UB**	LB>UB*
	M2	W>BS**	n.s	W>BS*	n.s	LB>UB*	LB>UB**
	M3	n.s	n.s	W>BS*	n.s	LB>UB***	LB>UB**
Temperature							
Winter	M1	n.s	BS>W*	BS>W*	BS>W***	UB>LB*	UB>LB***
	M2	n.s	BS>W**	n.s	BS>W**	UB>LB*	n.s
	M3	BS>W***	BS>W***	n.s	BS>W*	UB>LB*	UB>LB***
Summer	M1	BS>W*	n.s	BS>W**	BS>W*	UB>LB***	n.s
	M2	n.s	BS>W**	n.s	n.s	UB>LB***	n.s
	M3	n.s	n.s	n.s	n.s	n.s	UB>LB**
BPC							
Winter	M1	W>BS***	W>BS***	W>BS***	W>BS***	n.s	n.s
	M2	W>BS***	W>BS***	W>BS***	W>BS***	n.s	n.s
	M3	W>BS***	W>BS***	W>BS***	W>BS***	LB>UB**	LB>UB**
Summer	M1	W>BS***	W>BS***	W>BS***	W>BS***	n.s	UB>LB***
	M2	W>BS***	W>BS***	W>BS***	W>BS***	UB>LB**	n.s
	M3	W>BS***	W>BS***	W>BS***	W>BS***	UB>LB*	UB>LB***
Organic matter							
Winter	M1	W>BS***	W>BS***	W>BS***	W>BS***	UB>LB*	UB>LB*
	M2	W>BS***	W>BS***	W>BS***	W>BS***	n.s	n.s
	M3	W>BS***	W>BS***	W>BS***	W>BS***	UB>LB*	UB>LB***
Summer	M1	W>BS***	W>BS***	W>BS***	W>BS***	UB>LB*	n.s
	M2	W>BS***	W>BS***	W>BS***	W>BS***	n.s	n.s
	M3	W>BS***	W>BS***	W>BS***	W>BS***	UB>LB***	n.s

***p≤ 0.001; **p≤0.01;*p ≤ 0.05; n.s: not significant

Table S3 Results of PERMANOVA analysis performed to compare total carbohydrates, proteins, lipids, and protein to carbohydrates ratio of wrack deposits between tidal levels (upper and lower), beaches (Levante and Peginas) and seasons (winter and summer).

Variable		**Carbohydrates**		**Proteins**		**Lipids**		**PRT:CHO**	
Source	df	**MS**	**PseudoF**	**MS**	**PseudoF**	**MS**	**PseudoF**	**MS**	**PseudoF**
Level (Le)	1	0.039	0.01	0.430	0.24	0.041	0.20	0.001	0.05
Beach (Be)	1	31.242	3.51	24.092	6.79	4.094	4.17	0.006	0.06
Season (Se)	1	14.705	3.38	5.228	0.51	4.888	3.02	0.012	0.86
Date (Da(Se))	4	4.345	11.42***	10.257	10.82***	1.620	12.52***	0.014	3.25**
LexBe	1	14.164	3.54	3.178	0.61	0.588	0.35	0.153	12.99*
LexSe	1	0.552	0.19	11.056	6.05	0.373	1.80	0.033	1.15
BexSe	1	1.235	0.14	1.040	0.29	6.402	6.52	0.015	0.16
LexDa (Se)	4	2.943	7.73***	1.829	1.93	0.207	1.60	0.029	6.66***
BexDa(Se)	4	8.908	23.41***	3.550	3.75*	0.982	7.60***	0.099	22.99***
LexBexSe	1	0.068	0.02	0.484	0.09	0.717	0.43	0.002	0.13
LexBexDa(Se)	4	4.001	10.51***	5.224	5.51***	1.661	12.85***	0.012	2.72
Residual	48	0.381		0.948		0.129		0.004	
Total	71								
Transformation		4th root		4th root		4th root		4th root	

***p<0.001; **p<0.01;*p< 0.05; n.s: not significant

Table S4 Results of the pair-wise tests of PERMANOVA analysis between the upper and lower band (UB and LB, respectively) of the wrack deposits within each season and beach for total proteins (PRT), carbohydrates (CHO), lipids (LIP), and protein to carbohydrates ratio (PRT:CHO).

Source		**PRT**		**CHO**		**LIP**		**PRT:CHO**
Season	Date	Levante	Peginas	Levante	Peginas	Levante	Peginas	Both beaches
Winter	M1	n.s	LB>UB**	LB>UB***	n.s	n.s	n.s	n.s
	M2	n.s	LB>UB*	n.s	UB>LB*	n.s	n.s	LB>UB***
	M3	LB>UB**	UB>LB*	LB>UB***	UB>LB*	LB>UB***	UB>LB***	n.s
Summer	M1	n.s	UB>LB**	n.s	UB>LB***	n.s	UB>LB*	n.s
	M2	UB>LB***	n.s	LB>UB***	UB>LB**	UB>LB*	n.s	UB>LB**
	M3	UB>LB**	n.s	n.s	LB>UB**	n.s	n.s	UB>LB**

***p<0.001; **p<0.01;*p< 0.05; n.s: not significant

Table S5 Total abundance (nº indv) of arthropods found in wrack-covered (W) and bare sand (BS) areas during winter and summer on both beaches (Peginas and Levante)

	Peginas				Levante			
	Winter		Summer		Winter		Summer	
Taxa	BS	W	BS	W	BS	W	BS	W
Amphipoda								
Talitrus saltator (Montagu, 1808)	20	10	-	16	10	102	2	165
Deshayesorchestia deshayesii (Audouin,1826)	1	5	-	6	1	-	-	-
Isopoda								
Tylos europaeus (Arcangeli, 1938)	-	3	-	2	-	-	-	-
Coleoptera								
Tenebrionidae								
Phaleria bimaculata (Linnaeus, 1767)	-	-	-	32	-	3	-	68
Larvae tenebrionidae	-	-	2	11	-	-	1	99
Staphylinidae								
Bledius unicornis (German, 1825)	-	-	-	-	-	-	-	1
Anotylus nitidulus (Gravenhorst, 1802)	-	2	-	-	-	-	-	-
Aloconota gregaria(Erichson, 1840)	-	-	-	-	-	2	-	-
Omalium rivulare (Paykul, 1789)	-	-	-	-	-	1	-	-
Scopaeus minimus (Erichson, 1839)	-	-	-	-	-	-	-	1
Carpelimus rivularis(Motschoulsky,1860)	-	-	-	-	-	2	-	29
Xantholinus linearis (Olivier, 1795)	-	-	-	-	-	-	-	1
Cafius xantholoma (Gravenhorst, 1806)	-	1	-	15	-	-	-	1
Phytosus spinifer (Curtis, 1838)	-	2	-	3	-	-	-	-
Remus sericeus (Holme, 1837)	-	-	-	17	-	-	-	-
Larvae Sthapylinidae sp1	-	-	-	7	-	-	-	-
Larvae Sthapylinidae sp2	-	-	-	22	-	-	-	-
Athicidae								
Anthicus cervinus (LaFerté-Senectére, 1849)	-	-	-	-	-	1	-	1
Curculionidae	-	-	-	-	-	7	-	-
Carabidae	-	2	-	-	-	1	-	-
Chrysomelidae	-	2	-	-	-	-	-	-
Elateridae								
sp1	1	-	-	-	1	-	-	-
Hydrophilidae								
sp1	-	-	-	-	-	-	-	42
Histeridae								
sp1	-	-	-	-	-	-	-	4
Scarabidae								
sp1	-	-	-	-	-	5	-	-
Araneae								
Dictynidae	-	2	-	-	-	3	-	-
Agelinidae	-	-	-	-	-	3	-	-

Table S5 Continued

	Peginas				Levante			
	Winter		Summer		Winter		Summer	
Taxa	BS	W	BS	W	BS	W	BS	W
Diptera								
Canacidae	-	7	-	-	-	3	-	4
Dolichopodidae	-	2	-	-	-	1	-	-
Ephydridae	1	9	-	-	1	2	-	-
Unknown larvae sp	3	2	3	16	3	-	-	8
Hemiptera								
Saldidae								
sp1	-	1	-	-	-	-	-	-
Cymicidae								
sp1	2	1	-	-	2	1	-	1
Himeptera								
Pteromalidae								
sp1	1	-	-	-	1	-	-	2
Total abundance	29	56	5	147	19	141	3	427
Total number of species	7	16	2	11	7	16	2	15

Table S6 Results from PERMANOVA tests performed on total density (N), species richness (S), and Shannon–Wiener (H) diversity index and arthropod assemblages between habitats (wrack and bare sand), tidal levels (upper and lower), beaches (Peginas and Levante) and seasons (winter and summer).

		N		**S**		**H**		**Assemblages**	
Source	df	MS	PseudoF	MS	PseudoF	MS	PseudoF	MS	PseudoF
Habitat (Ha)	1	394.01	119.92***	34.56	223.28***	11.03	43.85**	24151.00	20.45**
Level (Le)	1	3.62	0.43	0.14	0.48	0.42	3.22	5985.10	4.55
Beach (Be)	1	1.99	0.21	0.00	0.00	0.40	1.24	6182.00	3.84*
Season (Se)	1	0.94	0.20	0.02	0.03	0.01	0.02	9342.80	8.06
Date (Da(Se))	4	4.62	2.39*	0.57	3.02*	0.54	4.29**	1158.80	2.68***
HaxLe	1	21.51	2.99	1.51	7.85*	0.57	6.61	5374.50	4.95*
HaxBe	1	11.23	9.57*	0.48	56.35**	0.00	0.00	6305.90	6.41*
HaxSe	1	6.84	2.08	0.35	2.26	0.07	0.27	7469.30	6.32*
LexBe	1	3.16	1.90	0.95	8.31*	0.60	9.43*	2332.70	1.59
LexSe	1	2.09	0.25	0.52	1.73	0.24	1.83	5716.70	4.34
BexSe	1	12.25	1.32	2.02	2.68	1.17	3.62	3706.40	2.3
HaxDa(Se)	4	3.29	1.70	0.15	0.82	0.25	1.99	1181.20	2.73***
LexDa(Se)	4	8.37	4.33**	0.30	1.59	0.13	1.04	1315.60	3.05***
BexDa(Se)	4	9.31	4.82***	0.75	4.00**	0.32	2.56*	1609.20	3.73***
HaxLexBe	1	0.65	1.78	0.41	6.01	0.77	19.86**	2481.20	2.25
HaxLexSe	1	0.03	0.00	0.01	0.06	0.13	1.49	3368.30	3.09
HaxBexSe	1	0.15	0.13	0.07	8.19*	0.51	1.52	3181.40	3.23
LexBexSe	1	18.34	11.00*	1.29	11.33*	0.85	13.30*	2366.70	1.61
HaxLexDa(Se)	4	7.17	3.71**	0.19	1.02	0.09	0.68	1086.70	2.52**
HaxBexDa(Se)	4	1.17	0.61	0.01	0.04	0.34	2.67*	983.89	2.28**
LexBexDa(Se)	4	1.67	0.86	0.11	0.61	0.06	0.50	2153.60	1.96
HaxLexBexSe	1	3.58	9.84*	0.08	1.22	0.62	15.97**	1466.90	3.39***
HaxLexBexDa(Se)	4	0.36	0.19	0.07	0.36	0.04	0.31	1100.70	2.55**
Residual	240	1.93		0.19		0.13		431.89	
Total	287								
Transformation		log(x+1)		4th root		4th root		4th root	

Degrees of freedom (df) and MS=mean square are shown. ***p≤ 0.001; **p≤ 0.01;*p≤ 0.05

Table S7 Results of the the pair-wise comparisons of the five-way PERMANOVA performed to compared arthropod assemblages between habitats (wrack and bare sand) at the upper and lower levels within each season and beach.

Assemblages		**Wrack vs Bare sand**				**Upper vs Lower band**			
Season	**Date**	**Levante**		**Peginas**		**Levante**		**Peginas**	
		Upper	Lower	Upper	Lower	BS	W	BS	W
Winter	M1	*	n.s	n.s	n.s	n.s	*	n.s	n.s
	M2	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s
	M3	n.s	**	n.s	**	n.s	*	n.s	**
Summer	M1	**	***	n.s	**	n.s	**	n.s	n.s
	M2	***	***	*	n.s	n.s	***	n.s	*
	M3	***	**	*	*	n.s	***	n.s	n.s

***p≤ 0.001; **p≤0.01;*p ≤ 0.05; n.s: not significant

Table S8 Results of the PERMANOVA analysis performed to compare density of the main species between wrack bands (upper and lower) and beaches (Levante and Peginas) during summer.

Variable		***Talitrus saltator***		***Phaleria bimaculata***		**Tenebrionidae larvae**	
Source	df	MS	PseudoF	MS	PseudoF	MS	PseudoF
Level (Le)	1	8.45	12.22	3.34	9.59	7.00	23.72*
Beach (Be)	1	2.69	2.96	0.27	0.33*	4.32	13.41 ·
Date (Da (Se))	2	0.28	0.96	1.54	4.69	0.17	0.85
LexBe	1	2.46	1.45	0.57	1.84	5.56	14.67 ·
LexDa (Se)	2	0.69	2.38	0.35	1.06	0.29	1.49
BexDa(Se)	2	0.91	3.12*	0.82	2.50	0.32	1.63
LexBexDa (Se)	2	1.69	5.82**	0.31	0.94	0.37	1.92
Residual	60			0.33		0.19	
Total	71						
Transformation		4th root		4th root		4th root	

Degrees of freedom (df) and MS=mean square are shown. **p≤0.01;*p≤0.05; ·0.05< p< 0.06

COLONIZATION PATTERNS OF SUPRALITTORAL ARTHROPODS IN NATURALLY STRANDED WRACK DEBRIS ON ATLANTIC SANDY BEACHES OF BRAZIL AND SPAIN

Colonization patterns of supralittoral arthropods in naturally stranded wrack debris on Atlantic sandy beaches of Brazil and Spain.

ABSTRACT

On sandy beaches, an important small-scale natural disturbance is the stranding of organic materials (wrack) from adjacent coastal systems. In this study, wrack debris was manipulated, removing or not removing natural wrack accumulations, to analyse and quantify the colonization process by supralittoral macroinvertebrates after the stranding of natural wrack debris on the upper beaches. For a general analysis of this process, field experiments on wrack colonization were undertaken on Spanish and Brazilian Atlantic sandy beaches subsidized by wrack debris (seaweed and mangrove propagules, respectively). Our results showed that the colonization of natural wrack accumulations did not occurred in a predictable pattern (i.e. early to late), but instead species of different stages of succession (i.e. early, middle, and late) colonized wrack from the first three days after the stranding of natural organic debris. Moreover, univariate and multivariate analysis demonstrated that the colonization of strandlines was slower in southern Brazil (16-day period) than in south-western Spain (3-day period). This process was driven by changes in the densities of Talitridae, Staphylinidae, and Tenebrionidae species in both regions. Moreover, beetles of Cleridae and Nitidulidae also contributed to colonizer community in southern Brazil (Paraná region). Our results suggest that the temporal variability of wrack biomass on the upper beach, the species-specific adaptations (i.e. mobility), and the strategies to use wrack debris as refuge and/or feeding sites could explain the different colonization patterns of assemblages in both Atlantic regions. The present study represents the first report of the colonization process by supralittoral arthropods in natural strandlines, and indicates the different ability of assemblages to colonize wrack debris naturally stranded on the Atlantic upper beaches of Brazil and Spain.

Keywords: wrack, colonization, macrofauna, beach, Atlantic coast, south of Brazil, southwest of Spain.

INTRODUCTION

The stranding of allochthonous organic materials (i.e. wrack) is considered an important factor structuring local invertebrate assemblages in marine intertidal systems (Valiela and Reitsma, 1995; Ford et al., 1999; Rossi and Underwood, 2002; Colombini and Chelazzi, 2003). Since disturbance is defined as an irregular event that causes structural changes in natural communities (Sousa, 1984; Pickett and White 1985; Platt and Connell, 2003), the stranding of wrack from adjacent coastal ecosystems (rocky intertidal, algal beds, seagrass meadows, mangroves etc.) is regarded as a small-scale natural disturbance in intertidal habitats (Inglis, 1989; Ford et al., 1999; Rossi and Underwood, 2002; Olabarria et al., 2007). Disturbance by wrack is severe on exposed sandy beaches because of their almost complete lack of *in situ* primary production (McLachlan and Brown, 2006). Wrack debris deposited on the beach provides food and/or refuge to a diverse and abundant component of the macrofaunal communities, mainly arthropods inhabiting the upper shores (such as talitrid amphipods, oniscoid isopods, coleopterans, arachnids, etc.) and, therefore, its availability is considered the main factor structuring supralittoral communities (Inglis, 1989; Colombini et al., 2000; Jedrzejczak, 2002b; Gonçalves and Marques, 2011). Wrack debris is transported from surrounding ecosystems associated with offshore dynamics and physical factors such as currents, prevailing winds, waves, and tides, which leave and distribute the materials along the intertidal zone (e.g. Ochieng and Erftemeijer, 1999; Orr et al., 2005). Consequently, wrack deposits are temporally and spatially heterogeneous, and thus are the distribution and zonation of supralittoral invertebrates (Stenton-Dozey and Griffiths, 1983; Jaramillo et al., 2006; Olabarria et al., 2007). Because many of these organisms form the bottom of coastal food chains, the availability of allochthonous input to support their biomass is a key factor in the abundance and diversity of marine and terrestrial ecosystems (Polis and Hurd, 1996; Spiller et al., 2010).

Wrack patches deposited on the upper beach, where it lies beyond the reach of the wave action, tend to remain on the beach surface for long periods and can be colonized by supralittoral macroinvertebrates. This process could be driven by trophic and shelter needs of the different colonizer species, and be influenced by the colonising and competitive abilities as well as the mobility of different taxa (Griffiths and Stenton-Dozey, 1981; Inglis, 1989; Marsden, 1991; Colombini et al., 2000; Olabarria et al., 2007; Dufour et al., 2012). Therefore, faunal colonization (i.e. the arrivals of species to

a patch of new habitat) determines the temporal changes in composition and structure of macroinvertebrates associated with wrack debris. Previous studies have evaluated the colonization and successional dynamics in wrack patches during the decay of organic matter. Lavoie (1985) reported that the colonization and replacement of macroinvertebrate species in natural (i.e. stranded by tides) decaying algae patches exhibited three successional stages: early (flies and amphipods), middle (staphylinid, hydrophylid bettles, fly larvae, spiders, etc.) and late (tenebrionids and histerids). Others studies have evaluated this process using litterbags (Inglis, 1989; Jędrzejczak, 2002b; Dufour et al., 2012) or artificial algal patches (Olabarria et al. 2007; Garrido et al., 2008; Rodil et al., 2008). Generally, talitrid amphipods and dipterans are reported as primary colonizers of algal patches, while different insect species, mainly coleopterans (e.g. staphylinids, tenebrionids, ptiliids, histerids, etc.) and spiders, tend to colonize drift seaweed days after the initial wrack deposition. Nevertheless, wrack debris that had been naturally stranded are highly variable, because the specific habitat attributes of wrack debris change temporally as these undergo the dynamics of the beach environment (i.e. stranded and ageing or re-deposited and re-exposed in successive tides). Therefore, natural strandlines are composed by wrack patches with different stages of ageing (i.e. from new and fresh materials to dry and decomposed materials), patch-size, thickness, etc., and, consequently, with different habitat attributes, that can increase the range of habitats available for supralittoral arthropods. A wide range of colonizer species can be expected in natural wrack debris, depending on their physiological tolerance (Lavoie, 1985) and their preference for a specific microhabitats and/or food sources (Pennings et al., 2000; Rodil et al., 2008; Colombini et al., 2011).

After the stranding of wrack debris, a directional change in assemblages could be expected: from early species associated with fresh wrack debris to early, mid and late successional species associated with patches of different states of ageing accumulated on the driftlines in successive tides. However, it is possible for the community structure to be similar at different times after the wrack accumulation, because species of different stages (i.e. early, middle and late) could colonize wrack deposits with different habitat features at natural strandlines; therefore, the directionality after a natural disturbance (i.e. the stranding of natural wrack debris) could be non-predictable (e.g. Platt and Connell, 2003). Nevertheless, no experimental field studies have manipulated strandlines to analyse the way in which these wrack accumulations are colonized by supralittoral arthropods. Besides the lack of colonization studies in natural strandlines, it

should be noted that no study has evaluated the colonization patterns of supralittoral macroinvertebrates associated with mangrove-propagule debris, which represents the main organic component of the strandlines in tropical and subtropical beaches (e.g. Colombini and Chelazzi, 2003; Ruiz-Delgado et al., 2014).

In this study, we investigated the colonization process by supralittoral arthropods at naturally strandlines. For this, we manipulated the presence of stranded wrack, removing or not removing wrack debris, from areas where these had naturally stranded, and then monitored the macroinvertebrates associated with wrack debris after the stranding of wrack on the supralittoral zone of sandy beaches. We analysed and quantified the colonization process comparing the standing stock of wrack debris and the community structure between recovered (manipulated) and control (unmanipulated) plots for a 47-day period. Specifically, we evaluated: (1) whether a directional change in assemblages could be triggered after the stranding of natural wrack debris; (2) the temporal changes in assemblages and their stabilization (i.e. the time of community restructuring compared to the control) after the accumulation of wrack debris in the strandlines. Moreover, we investigated (3) whether, disregarding the species differences, there would be similar colonization patterns in response to the stranding of natural wrack debris on Atlantic sandy upper beaches of the southern Brazil and south-western Spain.

MATERIALS AND METHODS

Study area

This study was conducted on four sandy beaches located in two geographical regions (Fig. 1): South of Brazil (Paraná-PR) and Southwest of Spain (SW Spain), in order to investigate, in a general way, colonization patterns of supralittoral macroinvertebrates in natural strandlines. These regions showed different types of allochthonous subsidies. The studied beaches from Paraná region were subsidized mainly by mangrove propagules, while selected beaches from SW Spain were subsidized by seagrasses and macroalgae.

The coast of the Paraná region (PR-south of Brazil) has a humid subtropical climate with a mean annual temperature of 22.2º C and mean annual precipitation of 1890 mm. Tides on the Paraná coast are semidiurnal and microtidal, with a tidal range between 0.5 and 2 m (Knoppers et al., 1987). Cem (25º 34´24´´S; 48º 20´13´´W) located

near to the mouth of the Paranaguá estuary, is a low-energy reflective beach, modified by tides. It has fine sands and a gentle slope. Assenodi (25º 35´24´´S; 42º 22´04´´W) located at Leste coastal plain, is an intermediate to dissipative, wave-dominated beach with fine sands and a gentle slope (Table S1). Both beaches are bordered by *restinga* (i.e. coastal sand dune vegetation). Wrack deposits of these studied beaches were composed of three types of mangrove propagules: *Laguncularia racemosa* (23%), *Rhizophora mangle* (21%) and *Avicennia schaueriana* (15%) as well as by terrestrial-derived vegetation (40%).

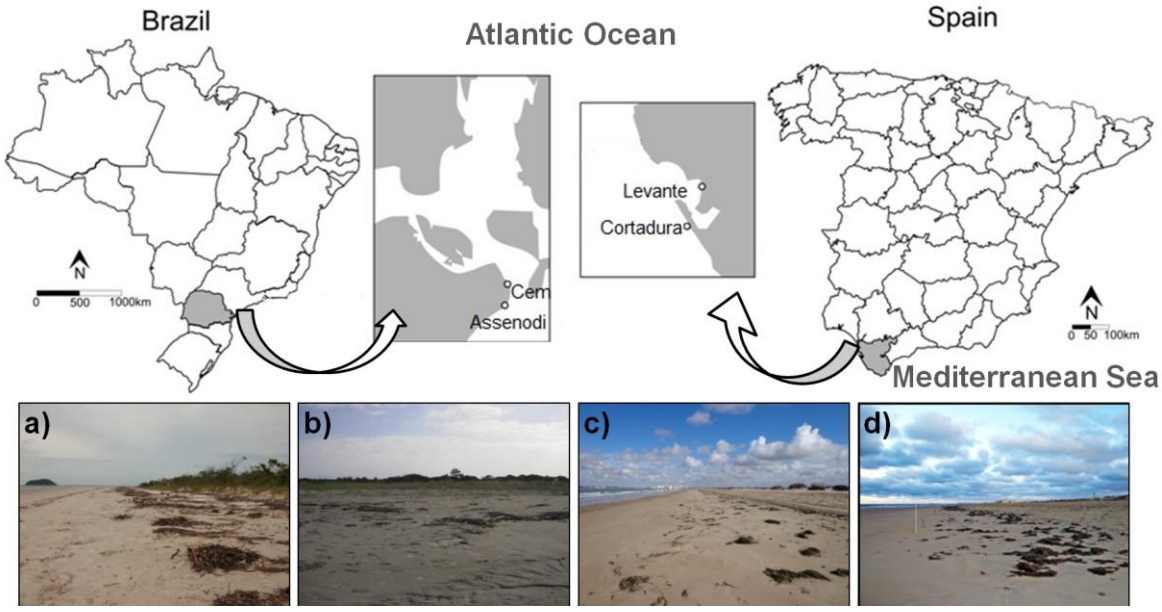

Figure 1.Geographic location of the study site on the southern coast of Brazil and the southwest coast of Spain, showing the four sandy beaches sampled: Cem (a) and Assenodi (b) (PR region); Levante (c) and Cortadura (d) (SW region).

The southwest of Spain (SW Spain) coast has a dry-summer subtropical climate with a mean annual temperature of 18.4º C and mean annual precipitation of 546.1 mm. The Gulf of Cadiz is a semidiurnal mesotidal environment with a tidal range between 3.2 and 1.1 m (Benavente et al., 2002). Levante (36º 33´37´´N; 6º 13´27´´W) located in the outer zone of Cadiz Bay, is a dune-backed, wave-dominated, and dissipative beach. It is characterized by medium sand and gentle slope (Table S1). Cortadura (36º28'58''N; 6º15'77''W), located at south of the Cadiz Bay, is a wave-dominated and intermediate beach. This beach has fine sand and gentle slope (Table S1) and is backed by foredunes and low vegetated dune ridges. The driftlines of Levante were composed

of two seagrass species: *Zostera noltii* (60%) and *Cymodocea nodosa* (40%). Meanwhile at Cortadura wrack deposits were composed by a mixture of brown macroalgae (66%) such as *Dictyopteris membranacea* and *Cladostephus spongiosus*, several species of red algae (29%) such as *Halopithys incurva* and *Chondria dasyphylla* and green algae (5%) such as *Codium decorticatum* and *Codium fragile.*

Study design and sampling methods

The *in situ* colonization in naturally accumulation of wrack debris was analysed on a 47-days period from 18 June to 3 August 2012 in the PR region and for 28 October to 13 December 2012 in the SW region. During these months (i.e. autumn season) climatic conditions were quite similar at both regions (Table S1). An experimental area 115 m long was delimited and divided into three sampling blocks at each beach. Each block consisted of two plots, control and recovered, each of 15 m wide, extending from the base of the dune to the driftline at each beach (c.a. 30-50m). Plots into each block were placed 5 m apart and the same distance was placed between blocks. Control plots were no manipulated and represent the unaltered condition of the wrack-associated fauna in the beach. However, recovered plots were manipulated previously to the start of the experiment (day 1), removing all macroscopic organic material accumulated on the beach surface (i.e. supratidal and intertidal) with the aid of garden rakes, to evaluate the colonization process in naturally stranded wrack debris covering an area without previous wrack accumulation at the upper beach.

Biological responses were compared between recovered and control plots on six sampling days (1, 3, 6, 16, 32 and 47 days) after the deposition of new wrack debris. Samplings were performed during low tides, when MHWS (mean high water spring tide) varied between 1.4-1.6 m on PR region and 1.2-1.5 m on SW Spain region and wrack debris were stranded on and above the current high tide-line of the beaches studied.

On each sampling date, wrack coverage was measured from photographs taken within six 1x1 m quadrats placed randomly in each plot. Moreover, at each plot, random samples (n=6) were collected pushing a core (15 cm in diameter and 20 cm in depth) vertically through the wrack mat into the sediment to collect wrack debris as well as associated macrofauna and macrofauna underneath the wrack debris. Samples were taken within each photographed quadrat. At the free end of the core, a plastic bag was

used to prevent mobile fauna (mainly insects and amphipods) from escaping. Samples were transferred into 70% alcohol. In the laboratory, the samples were washed to separate fauna and wrack debris. All macroinvertebrates retained on a sieve of 0.5 mm mesh were sorted, counted and identified to the highest possible taxonomic level. For each biological sample, species number, density (expressed as total number of individuals per m^{-2} of the surface covered by wrack debris), and diversity (Shannon-Wiener index) were calculated. All wrack debris of each sample was separated and dried to a constant weight at 60ºC (g dw). The coverage was estimated as the percentage of plot surface (1x1 m quadrat) covered by wrack debris using Image J (v. 1.45) (Abràmoff et al., 2004). For estimate the amount of stranded wrack in each plot (g dw/m^2), the values of biomass per core and coverage of each sampling date were used.

Data analysis

As our main goal was to search for colonization patterns of the supralittoral assemblages in response to the stranding of wrack, univariate and multivariate analyses were performed separately for each region (PR and SW). Spatial and temporal changes in wrack biomass and univariate descriptors (total density, species richness and Shannon-Wiener´s index) were evaluated using a mixed analysis of variance model including four factors: treatments (2 levels: control and recovered, fixed and orthogonal), sampling times (6 levels, fixed and orthogonal), site (2 levels, fixed and orthogonal), and blocks (3 levels, random and nested in each site). Homogeneity of variance was examined by Cochran's test and normality was analysed through visual inspection of residual and probability plots. Data were transformed if variances were significantly different at p=0.05. When heterogeneity persisted, analyses were done on untransformed data; but the p-values for the F-ratios were considered significant at p <0.01 (Underwood 1997). Where ANOVA indicated a significant difference for the main factors or their interactions, the source of difference was identified using Student-Newman-Keul (SNK) tests (Underwood, 1997).

A permutational multivariate ANOVA (PERMANOVA, Anderson, 2001) based on the same design used for the univariate analyses was performed to analyse the spatial and temporal changes of macroinvertebrate assemblages structure after the deposition of natural wrack debris on studied beaches. Only significant effects ($p<0.05$) were further investigated through a series of *a posteriori* pair-wise comparisons. The similarity matrices were calculated using the Bray–Curtis coefficient based on fourth-root

transformed data. The statistical significant of variance components were tested using 9999 permutations and a significance level p=0.05; whether the number of possible permutations were lower than 150, the Monte Carlo p-value (p (MC)) was used. The contribution of individual species to overall dissimilarity in assemblage structure between treatments and times was determined by SIMPER analysis. Non-parametric multidimensional scaling (MDS) based on distance of centroides was used to visualize the temporal changes in assemblages between treatments on studied beaches from each region (Clarke and Warwick, 1994). Univariate analyses were performed using the GAD package (Sandrini-Neto and Camargo, 2013) in R 2.15.2 (R Development Core Team, 2012) and multivariate analyses were carried out using the PRIMER v.6 with the PERMANOVA+ add on (PRIMER-E Ltd., Plymouth, UK).

RESULTS

Standing stock of wrack debris

The standing stock of wrack debris varied between treatments and showed different temporal and spatial patterns in each study region. In the Paraná region, the wrack biomass varied significantly between treatments and this variation differed between blocks within each beach from time to time (i.e. significant Treatment×Beach×Block×Time interaction, Table 1). Despite of the small-scale spatial variability, wrack biomass was accumulated in recovered areas between days 1 and 3 at Cem, although its values were lower than in control plots (SNK for all blocks, $p < 0.05$; Fig. 2a). Similar values compared to controls were detected on day 6 (Fig. 2a). The same pattern was recorded on days 1, 3, 6, and 16 at Assenodi beach, although with much far lower values compared to controls (SNK for all blocks, $p < 0.001$; Fig. 2b), reaching the control values between days 16 and 32 (Fig. 2b).

In the SW Spain region, the wrack biomass differed between treatments and this pattern varied between beaches and over time (i.e. significant Treatment×Site×Time interaction, Table 1). At Levante beach, wrack debris were accumulated between days 1 and 3 in the recovered areas, and this increased between days 3 and 6, although its values were lower than in control plots (SNK tests, $p < 0.001$, Fig. 2c). Values similar to those of the control areas were detected on day 6. The same pattern was observed between days 1 and 3 in the recovered areas of Cortadura beach (SNK test, $p<0.001$ on day 1; Fig. 2d), reaching values comparable to the controls on day 3.

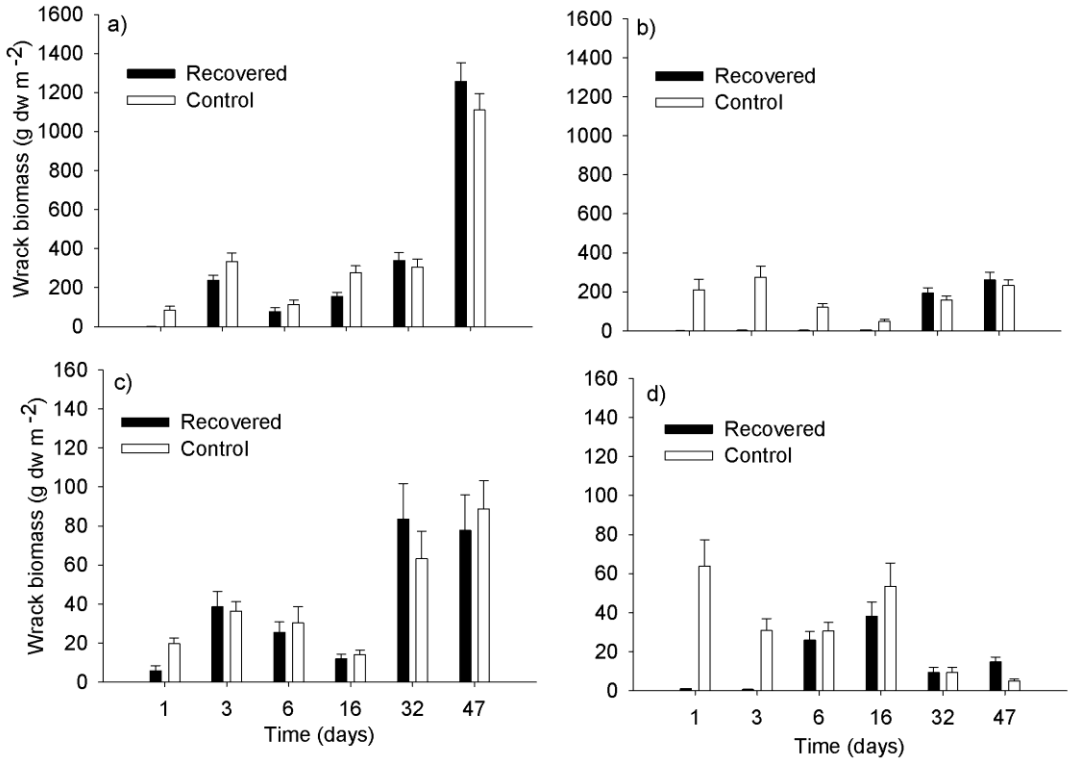

Figure 2. Mean (± S.E, n=18, average of treatment plots) of wrack biomass (g dw/ m^2) in the control and recovered plots at (a) Cem and (b) Assenodi (PR region) and (c) Cortadura and (d) Levante (SW Spain region) over time.

Colonization patterns of supralittoral macroinvertebrates in wrack debris

Univariate patterns of supralittoral assemblages

In the Paraná region, a total of 4514 individuals and 23 taxa were sampled in wrack deposits on both beaches. The talitrid amphipod *Platorchestia monodi*, the staphylinids of genus *Bledius* and coleopterans Cleridae, Nitidulidae, and Tenebrionidae accounted for 85% of the total abundance associated with wrack debris, although the contribution of these taxa in the community structure differed at each beach (Table S2). *Platorchestia monodi*, *Bledius bonariensis*, *Bledius* sp1, Carabidae at Assenodi; *Platorchestia monodi*, Cleridae, Nitulidae, and *Phaleria testacea* at Cem colonized wrack debris within 1 and 3 days after the stranding of natural wrack. The talitrid *P. monodi* initially occupied wrack debris in very low numbers as well as the coleopterans (Cleridae, Carabidae Nitulidae, etc.), and their abundances were low with respect to the control plots (Table 2). On the contrary, *B. bonariensis* colonized wrack debris in high numbers and its abundance was even higher than in the control plots, although this

pattern was detected only on Assenodi (Table 2). Moreover, Coleoptera larvae, Diptera and Lycosidae occupied wrack debris within 1 and 3 days, but in low abundances (Table 2). The following days of exposure (i.e. between days 6 and 47), *P. monodi* was found in high abundance in wrack debris of the recovered areas, while coleopterans (such as Cleridae, Carabidae, Nitidulidae), Diptera and Lycosidae were also found, though in low abundance.

Table 1 Results of the mixed-model ANOVA for the wrack biomass between treatments (2 levels; fixed factor), times (6 sampling days; fixed factor), sites (2 levels; fixed factor) and blocks (3 levels; random factor) in each geographical region (PR-Paraná and SW-Southwest of Spain). df=degrees of freedom; MS=mean square; ***p<0.001; **p<0.01 and *p< 0.05.

Wrack biomass					
Source		**SW region**		**PR region**	
	df	MS	F	MS	F
Treatment=Tr	1	11.27	63.13**	1782.02	8.30*
Site=Si	1	14.82	9.00*	5255.20	107.61***
Time=Ti	5	2.22	3.17*	3329.07	130.45***
Block=Bl (Si)	4	1.65	8.26***	48.84	3.56**
TrxBe	1	4.06	22.72**	419.25	1.95
TrxTi	5	5.34	24.37***	360.90	9.12***
BexTi	5	10.56	15.07***	957.41	37.52***
TrxBl (Si)	4	0.18	0.90	214.60	15.63***
TixBl (Si)	20	0.70	3.52***	25.52	1.86*
TrxBexTi	5	2.76	12.61***	85.72	2.17
TrxTixBl (Si)	20	0.22	1.10	39.59	2.88***
Residual	360	0.20		13.73	NA
Cochran's test		C = 0.0549; n.s.		C = 0.0547; n.s.	
Transformation		Fourth root		Square root	

In the SW region of Spain, a total of 7193 individuals classified in 31 taxa were collected in wrack debris during the experiment. The talitrid amphipod *Talitrus saltator*, the staphylinid *Phytosus spinifer*, the tenebrionid *Phaleria bimaculata* and larvae of this family, and dipterans were the most abundant taxa (representing ~ 80% of the total abundance) associated with algal wrack debris. However, the contribution of these taxa in the community structure differed between beaches (Table S3). Colonization of new wrack debris was initiated by *Talitrus saltator*, *Tylos europaeus*, *Phaleria bimaculata*, dipterans (adults and larvae) and staphylinid species (*Phytosus spinifer* and *Aloconota*

gregaria), which colonized wrack debris within 1 and 3 days after the stranding of natural wrack (Table 3). On the following days of exposure (i.e. between days 6 and 47), *T. saltator* was found with high abundance values in wrack debris, while *T. europaeus*, *P. bimaculata*, dipterans (adults and larvae) and staphylinid species were also caught, although with low abundance in recovered areas (Table 3).

The colonization pattern depended on the univariate community indices used. In the Paraná region, the mean total density differed significantly between treatments and this pattern changed between beaches and over time (i.e. significant Treatment×Site×Time interaction; Table 4). The mean total density increased between days 1 and 3 in the recovered areas, although values were lower than in control areas (SNK tests $p<0.05$; Fig. 3a, b), and values became similar to those of the control areas on days 3 and 6 at Assenodi and Cem, respectively (Fig. 3a, b). Otherwise, the number of species and diversity varied between treatments and over the time (i.e. significant Treatment×Time interaction; Table 4). In the recovered areas, both variables increased between days 1 and 3, but decreased between days 3 and 6, with low values than control areas (SNK test $p<0.05$; illustrated for Cem beach, Fig. 3c, d). Similar values compared to the control areas were detected on day 16 at both beaches (SNK test $p>0.05$). On the other hand, in the SW region, total density differed significantly between treatments and this pattern was consistent between beaches and time (i.e. no significant interactions; Table 5). Total density was lower in recovered than in control areas over the time (SNK tests for all times $p<0.01$; Fig. 4a). However, the number of species and diversity varied between treatments and this pattern changed between beaches and over time (i.e. significant Treatment×Site×Time interaction; Table 5). At Levante beach, the number of species and diversity was lower in recovered than in control areas on day 3 (SNK test, $p<0.01$; Fig. 4b, d), whereas species richness showed the same pattern on days 1 and 6 (SNK test, $p<0.05$; Fig. 4c) at Cortadura beach, while diversity did not differ between treatments on this beach (SNK test, $p>0.05$).

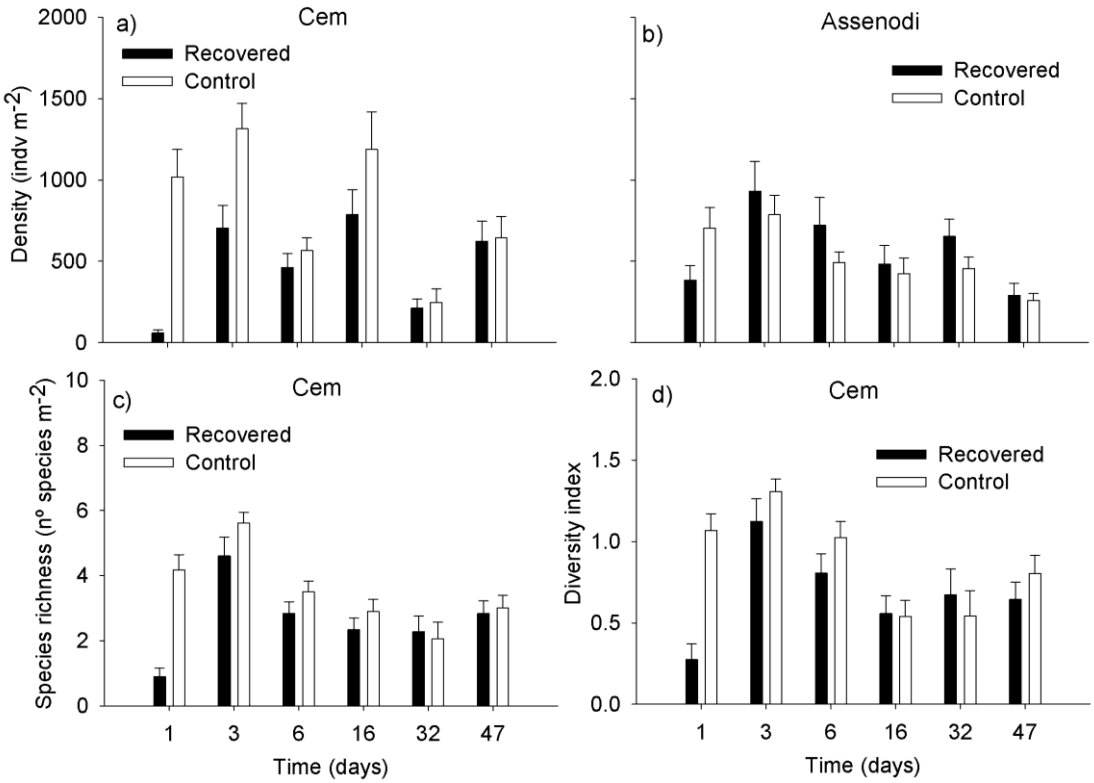

Figure 3.Mean (± S.E, n=18, average of treatment plots) of (a, b) total density in the control and recovered plots at Cem and Assenodi over time; (c) species richness and (d) diversity index in the control and recovered plots at Cem over time.

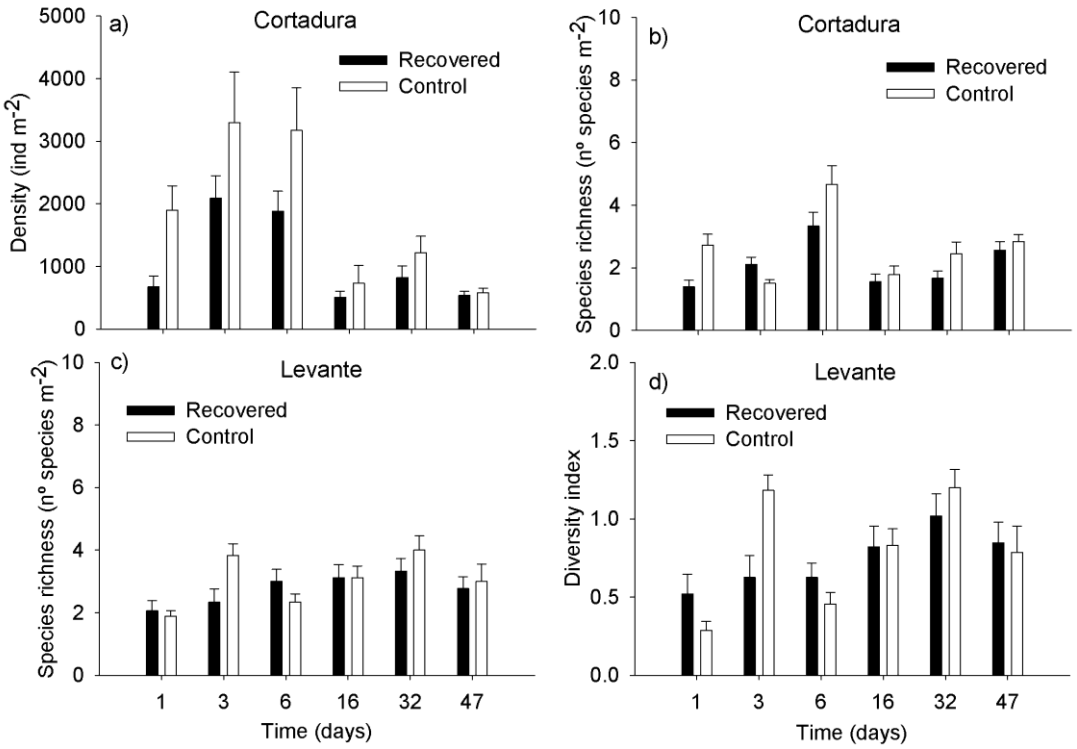

Figure 4. Mean (± S.E, n=18, average of treatment plots) of (a) total density in the control and recovered plots at Cortadura over time; (b,c) species richness and (d,f) diversity index in the control and recovered plots at Cortadura and Levante over time.

Table 2 Temporal variation of macroinvertebrate taxa based on abundance classes (4th root transformed) for each treatment on sandy beaches from Paraná region (PR).

Abundance	Recovered (days)						Control (days)					
class	1	3	6	16	32	47	1	3	6	16	32	47
4.0-4.5										Pla		
3.5-4.0		**Bon**		Pla			Pla	Pla				
3.0-3.5		Pla	**Bon**		**Pla**	Pla	**Pla**	**Pla**				Pla
2.5-3.0	**Bon**	**Car**	Pla Nit **Car**	Cle **Pla**		**Pla**	Nit Pha	Cle Nit **Bon**	Pla Nit **Pla**	**Pla**	**Pla**	Nit **Pla**
2.0-2.5	**Eff**	Cle Nit	Cle	Nit **Bon** **ColLv** **Car**	**Bon** **ColLv**	ColLv Nit	Cle **Nit** **Bon**	Dip **Car**	Cle **Bon**	Nit Cle	Pha **Bon**	
1.5-2.0	**Ble** **ColLv** **Car**	Pha TenLv Dip **Pla**	**Ble** **Pla**	Pha **Eff**	Pla Cle Pha Dip Ble **Car**	Dip **Car**	TenLv **Ble** **Car**	Pha TenLv Bon Ara **Nit** **Ble**	Pha TenLv **Nit** **ColLv** **Car**	Dip **Cle** **ColLv** **Bon**	Pla Cle Dip TenLv **Cle** **Car** **ColLv** **Eff**	Cle Pha **Cle** **Car**
1.0-1.5	Cle TenLv Her	Bon Ble Ara ColLv **Eff**	Pha TenLv Dip Allo	Dip **Dip**	Her TenLv **Cle** **Nit** **Eff** **Allo** **Dip**	Cle Pha **Nit** **Bon** **Dip** **ColLv**	Her Dip Arc **Allo** **ColLv**	Her Ble Allo ColLv **Dip** **ColLv**	Dip **Allo** **Ble**	Pha Bon **Ble** **Dip**	Her Ble Ara ColLv **Nit** **Dip**	Her Dip ColLv **Nit** **Bon** **Allo** **Dip** **ColLv**
0.5-1.0	Bon ColLv **Pla**	Her Allo **Ble** **Allo** **Dip** **ColLv**	Ara **ColLv** **Eff**	**Cle** **Allo**	ColLv Allo	Bon Ble TenLv **Ble** **Allo**	Bon Allo **Dip**	**Eff**	Bon **Cle**	Allo **Eff**	Nit	Allo Ble TenLv **Ble** **Eff**

Pla -*Platorchestia monodi*; Pha -*Phaleria testacea*; Bon -*Bledius bonariensis*; Her -*Bledius hermani*; Dip-Diptera; Cle -Cleridae; Nit -Nitidulidae; TenLv -Tenebrionidae larvae; ColLv -Coleoptera Larvae sp1; Ble -*Bledius* sp1; Allo -*Allocosa brasiliensis*; Ara -Arachnidae sp1; Eff -*Efflagitatus* Larvae
Bold names correspond to **Assenodi** beach.

Table 3 Temporal variation of macroinvertebrate taxa based on abundance classes (4th root transformed) for each treatment on sandy beaches from Southwest of Spain region (SW).

Abundance class	Recovered (days)						Control (days)					
	1	3	6	16	32	47	1	3	6	16	32	47
5.0-5.5								**Tal**				
4.5-5.0		**Tal**	**Tal**				**Tal**		**Tal**			
4.0-4.5									**Phy**		**Tal**	
3.5-4.0	**Tal**		Tal		**Tal**		Tal			**Tal**		
3.0-3.5			**Phy**	**Tal**		**Tal**			Tal	DipLv		**Tal**
2.5-3.0	Tal			Tal				Tal Dip		Tal	Dip **Phy**	
2.0-2.5		Tal Dip		**Phy**	Dip **Phy**	Tal Lyn	**TenLv** **Phy**	DipLv	**TenLv**	Phy		Tal Dip **Phy**
1.5-2.0	Pha TenLv **TenLv** **Phy**	TenLv	Dip **Pha** **Lavt**	DipLv Phy TenLv **TenLv**	Tal Phy Psy	Dip Phy Psy **Dip** **Phy**	**Dip** **Tyl** **Pha**	Pha TenLv	Dip **Dip** **Tyl** **Pha** **Acro**	Pha TenLv **Tyl** **TenLv** **Phy**	Tal Psy **Dip** **TenLv**	Ano Lyn Psy **Dip**
1.0-1.5	Dip DipLv Alo **Dip**	Pha **Dip** **Tyl** **Alo** **Phy** **DipLv**	Alo **Dip** **Tyl** **Alo** **Caf**	Dip Pha Alo Caf **Pha** **DipLv**	Alo Ano **Lavt** **Caf**	Ano **Tyl** **TenLv** **Car** **Lyn**	Dip Car	Alo Phy **Dip** **Alo** **Phy**	DipLv Ano Car **Caf**	Alo Caf **DipLv**	TenLv Phy Ano **Pha** **Alo** **Ano** **Caf**	Alo Caf Car **TenLv** **Ano** **Caf** **Lyn**
0.5-1.0	Ano	DipLv Phy Lyn **TenLv** **Lyn** **Car** **Caf**	DipLv TenLv	**DipLv**	Caf Lyn **Acro** **Lyn**	Pha Alo Caf	DipLv Alo **Car**	Lyn **DipLv**	**Alo** **Car** **DipLv**	Dip Ano	Pha Caf Car **Acro** **Car** **Psy**	Pha Phy **Acro** **Psy**

Tal -*Talitrus saltator*; Tyl -*Tylos europaeus*; DipLv - Diptera Larvae; Dip - Diptera; Pha - *Phaleria bimaculata*; *TenLv -Tenebrionidae Larvae; Alo - Aloconota gregaria*; Phy - *Phytosus spinifer*; Ano - *Anotylus nitidulis*; Caf - *Cafius xantholoma*; Lyn - Lyniphiidae; Psy - Psylloidea; Car -Carabidae.
Bold names correspond to **Cortadura** beach

Table 4 Results of the mixed-model ANOVA for the community structure indices (total density, species richness, Shannon–Wiener index) and the densities of the main taxa (*Platorchestia monodi*, *Bledius bonariensis*, *Phaleria testacea*, Nitidulidae and Cleridae) at PR region between treatments (two levels; fixed factor), time (six sampling days; fixed factor), site (two levels; fixed factor) and block (three levels; random factor). df=degrees of freedom; MS=mean square; ***p<0.001; **p<0.01 and *p< 0.05.

PR region																	
Source		**Total density**		**Species richness**		**Diversity**		***P. monodi***		***B. bonariensis***		***P.testacea***		**Nitudulidae**		**Cleridae**	
	df	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Treatment=Tr	1	34.65	41.75**	70.08	26.24**	4.41	16.53*	39.24	37.34**	19.89	1.59	44307.00	3.55	90.80	31.94**	47.65	49.97**
Site=Si	1	25.91	3.94	21.33	4.94	1.91	9.96*	13.55	4.47	870.43	213.96***	161482.55	18.49*	366.33	39.29**	381.21	29.28**
Time=Ti	5	28.46	5.35**	28.03	10.77***	1.81	11.49***	5.56	3.33*	77.08	43.43***	12723.41	4.74**	36.76	8.15***	13.31	3.02*
Block=Bl(Si)	4	6.58	2.19	4.32	1.74	0.19	0.87	3.03	4.22**	4.07	1.54	8735.86	1.89	9.32	2.92*	13.02	4.39**
TrxBe	1	19.32	23.28**	1.12	0.42	0.00	0.00	0.00	0.00	37.05	2.97	39823.24	3.19	0.10	0.04	16.76	17.58*
TrxTi	5	19.54	10.21***	17.66	7.21***	1.28	5.73**	9.31	9.71***	1.73	0.60	15915.85	5.45**	31.30	8.18***	2.74	0.55
BexTi	5	24.28	4.57**	21.84	8.39***	1.04	6.58***	12.57	7.54***	42.06	23.70***	12460.36	4.64**	39.01	8.65***	27.33	6.20**
TrxBl(Si)	4	0.83	0.28	2.67	1.07	0.27	1.20	1.05	1.46	12.49	4.73***	12472.32	2.69*	2.84	0.89	0.95	0.32
TixBl(Si)	20	5.32	1.77*	2.60	1.05	0.16	0.71	1.67	2.32**	1.77	0.67	2682.78	0.58	4.51	1.41	4.41	1.48
TrxBexTi	5	8.19	4.28**	2.37	0.97	0.15	0.69	1.13	1.18	5.34	1.87	15270.19	5.24**	3.00	0.79	4.97	1.01
TrxTixBl(Si)	20	1.91	0.64	2.45	0.99	0.22	1.01	0.96	1.33	2.86	1.08	2921.92	0.63	3.83	1.20	4.94	1.66*
Residual	360	3.00		2.49		0.22		0.72		2.64		4625.74		3.19		2.97	
Cochran's test		C=0.055; n.s.		C=0.049; n.s.		C=0.0395; n.s.		C=0.039; n.s.		C=0.043; n.s.		C=0.301;n.s		C = 0.040		C=0.053; n.s.	
Transformation		ln (x+1)		-		-		log (x+1)		log (x+1)		-		log (x+1)		log (x+1)	

Table 5 Results of the mixed-model ANOVA for the community structure indices (total density, species richness, Shannon–Wiener index) and the densities of the main taxa (*Talitrus saltator*, and Tenebrionidae larvae) at SW region between treatments (two levels; fixed factor), time (six sampling days; fixed factor), site (two levels; fixed factor) and block (three levels; random factor). df=degrees of freedom; MS=mean square; ***p<0.001; **p<0.01 and *p< 0.05.

SW region											
Source		**Total density**		**Species richness**		**Diversity index**		***T. saltator***		***Tenebrionidae larvae***	
	df	MSx10^7	F	MS	F	MS	F	MS	F	MS	F
Treatment=Tr	1	2.20	24.36**	20.02	19.09*	0.54	5.20	19.29	27.25**	15.58	4.12
Site=Si	1	10.94	217.46***	35.02	14.09*	15.14	85.27***	641.03	329.41***	3.57	4.49
Time=Ti	5	1.86	9.98***	14.44	6.55***	1.28	5.48**	66.60	21.60***	18.46	4.31**
Block=Bl(Si)	4	0.50	0.35	2.48	1.05	0.18	0.96	1.95	0.50	0.80	0.28
TrxBe	1	0.85	9.42	2.52	2.40	0.06	0.59	0.29	0.41	0.01	0.00
TrxTi	5	0.16	3.06	0.95	0.47	0.18	0.86	13.99	3.10*	9.57	2.74*
BexTi	5	1.36	7.31***	24.52	11.11***	2.68	11.51***	30.54	9.91***	43.33	10.12***
TrxBl(Si)	4	0.09	0.64	1.05	0.44	0.10	0.57	0.71	0.18	3.78	1.34
TixBl(Si)	20	0.19	1.32	2.21	0.93	0.23	1.26	3.08	0.79	4.28	1.52
TrxBexTi	5	0.16	3.01	10.14	4.98**	0.65	3.06*	2.37	0.53	1.89	0.54
TrxTixBl(Si)	20	0.05	0.38	2.04	0.86	0.21	1.16	4.51	1.15	3.49	1.24
Residual	360	0.14		2.37		0.18		3.91		2.82	
Cochran's test		C = 0.270; p<0.01		C = 0.046; n.s.		C= 0.052; n.s.		C = 0.053; n.s.		C=0.049; n.s.	
Transformation		-		-		-		log (x+1)		log (x+1)	

Multivariate patterns of wrack-associated macroinvertebrate assemblages

In the PR region, PERMANOVA tests revealed a significant Treatment×Time interaction (Table 6). Analyses of pairwise comparisons of this interaction showed that wrack-associated macrofaunal assemblages in recovered plots differed from those in control plots on days 1, 3, and 6 (Table 6; Fig. 7a). This result indicated that the structure of the assemblages associated with wrack mangrove-propagule was re-established between 6 and 16 days. SIMPER analysis showed that dissimilarities of between treatments were accounted for Talitridae (*Platorchestia monodi*), Staphylinidae (*Bledius bonariensis*), Tenebrionidae (*Phaleria testacea*), and the coleopterans clerid and nitidulid (Table S4). The densities of *P. monodi* and nitidulid beetles varied between treatments and over time (i.e. significant Treatment×Time interaction; Table 4).

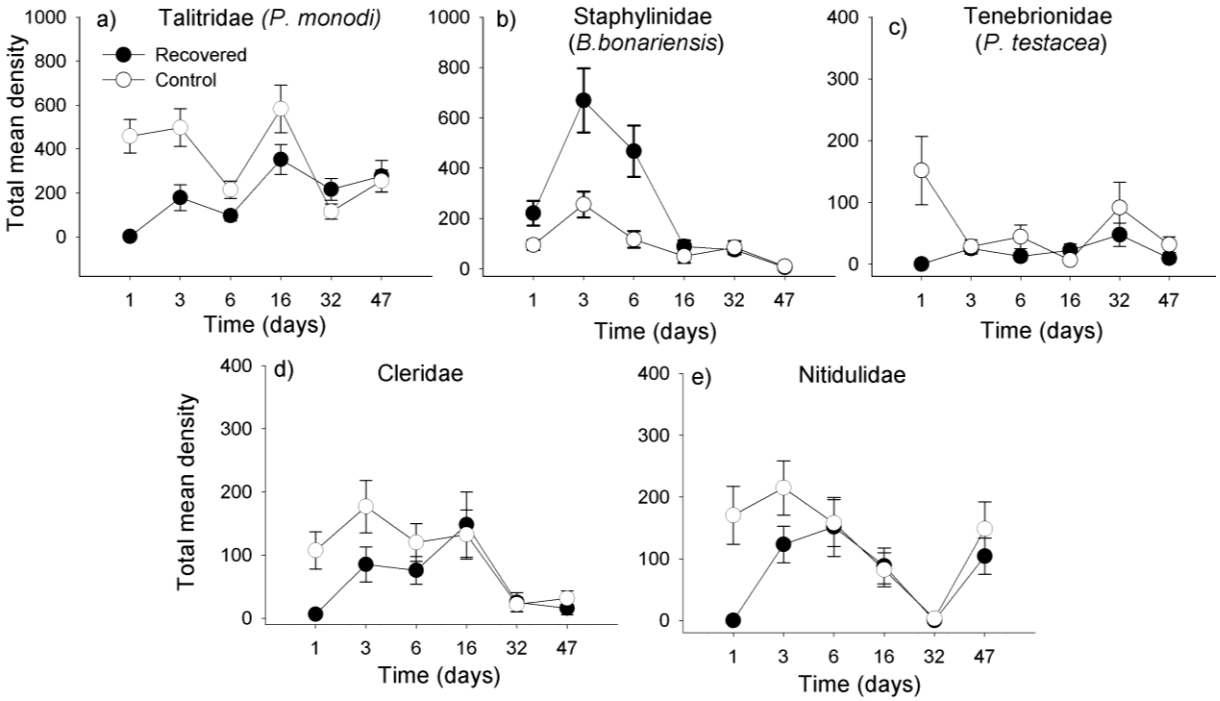

Figure 5.Mean (± S.E, n=18, average of treatment plots) density of individuals (nº indv./m^2 surface wrack-covered) in the control and recovered plots over time.(a) *Platorchestia monodi* average in the control and recovered plots at Cem (b) *Bledius bonariensis* average in the control and recovered plots at Assenodi (c) *Phaleria testacea* average in the control and recovered plots at Cem, (d) Cleridae, and (e) Nitidulidae average in the control and recovered plots at Cem.

An increase in *P. monodi* density was observed between days 1 and 6 in the recovered areas and the same pattern was observed for nitidulid density between days 1 and 3,

although with lower values than in control areas (SNK tests, $p<0.01$). Similar values compared to the control areas were detected on days 16 and 6, respectively (Fig. 5a, e). The density of *P. testacea* and clerid beetles varied between treatments and this pattern changed between beaches and over time (Table 4). Despite the small-scale spatial variability, the densities of both taxa were lower in recovered than in control areas on day 1 (SNK test, $p<0.05$; Fig. 5c,d), but only at Cem beach, although clerids showed this pattern also on days 3 and 6 (SNK test, $p<0.05$). Clerids reached similar density values compared to the control areas on day 16 (Fig. 5d). On the other hand, the density of *B. bonariensis* varied between treatments and this pattern varied between blocks within each beach (i.e. significant Treatment×Site (Block) interaction; Table 4). *B. bonariensis* density was lower in recovered than in control areas, but only at Assenodi beach (SNK test $p<0.05$; Fig. 5b). Moreover, this pattern was clear between 1 and 6 days but, due to the small-scale spatial variability, did not show statistically significant differences between treatments over time (Fig. 5b).

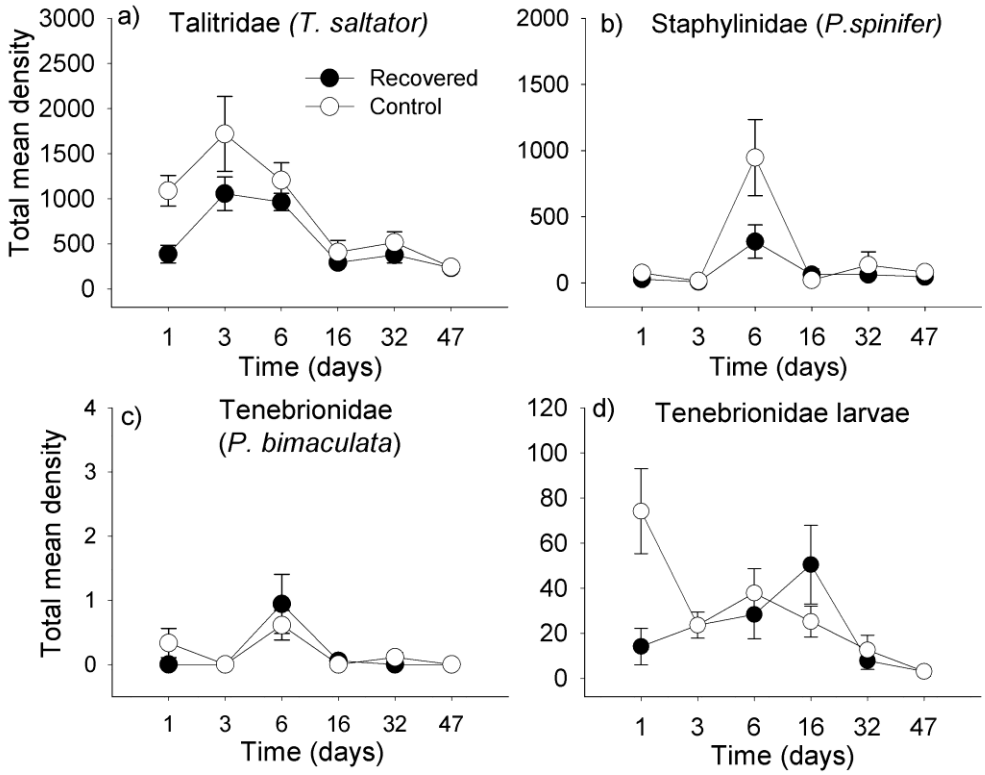

Figure 6. Mean (± S.E, n=18, average of treatment plots) density of individuals (nº indv./m^2 surface wrack-covered) in the control and recovered plots over time.(a) *Talitrus saltator* average in the control and recovered plots at Levante and Cortadura (b) *Phytosus spinifer* average in the control and recovered plots at Cortadura (c) *Phaleria bimaculata* average in the control and recovered plots at Levante, (d) Tenebrionidae larvae average in the control and recovered plots at Levante.

In SW Spain, wrack-associated macrofaunal assemblages in recovered plots differed from those in controls over time and this pattern varying between beaches (i.e. significant Treatment×Beach×Time interaction). Pairwise comparisons on this interaction revealed that the community structure differed between treatments on day 1 and these differences were not recorded on day 3 at both beaches (Table 6; Fig. 7b). This result indicated that the structure of wrack-associated fauna was re-established between days 1 and 3. Moreover, the magnitude of the change between arthropod assemblages in control and recovered areas differed between beaches, but these differences were not statistically significant. SIMPER analysis showed that Talitridae (*Talitrus saltator)*, Tenebrionidae (*Phaleria bimaculata* adults and larvae of this family) Staphylinidae (*Phytosus spinifer)* and Diptera were the main taxa responsible for the differences in the community structure between the recovered and control plots (Table S3).

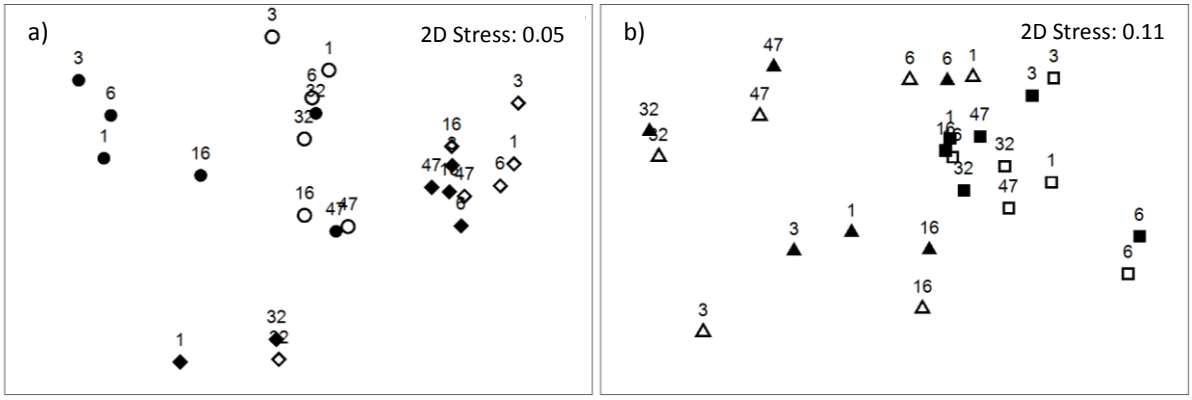

Figure 7. Ordination (nMDS) of centroids derived from Principal Coordinate Analysis (PCO) for the combination of factors: Treatment (control vs. recovered), Time (1, 3, 6, 16, 32, 47 days) and Beach (Cem and Assenodi-PR region; Cortadura and Levante-SW region). a) Paraná region: ○ Assenodi control; ● Assenodi recovered; ◇ Cem control; ◆ Cem recovered; b) SW Spain region: ▲ Levante recovered; △ Levante control; ■ Cortadura recovered; □ Cortadura control.

The density of *T. saltator* varied between treatments over time (i.e. significant Treatment×Time interaction; Table 5). *T. saltator* density was lower in recovered areas than in control areas on day 1 (SNK tests $p<0.01$, Fig. 6a), reaching values similar to those of the control areas on day 3 (Fig. 6a). *P. bimaculata* and tenebrionid larvae were found in wrack debris of recovered areas on day 1, although with lower values than in control areas (Fig. 6 c,d). However, this pattern was significant only for Tenebrionidae larvae (SNK tests $p<0.001$; Fig. 6d) and reached values similar to those of the control

areas on day 3 (Fig. 6d). On the other hand, *P. spinifer* appeared less abundantly in recovered areas than in control areas after 1 and 3 days of the stranding of wrack debris, respectively; however, because colonization was very quick, it was not possible to detect significant temporal variations in its densities between treatments (i.e. non-significant interaction Treatment × Time; Fig. 6b).

Table 6 PERMANOVA results and pairwise comparisons performed to compare arthropods assemblages following the same sources of variation for each geographical region (PR-Paraná and SW Spain region). Degrees of freedom (df), MS=mean square and Pseudo-F are shown. The data were fourth root transformed. ***p<0.001; **p<0.01; and *p< 0.05. Bold values correspond to significant results.

Assemblages					
Source		**SW region**		**PR region**	
	df	MS	Pseudo-F	MS	Pseudo-F
Treatment=Tr	1	2242.00	5.63*	22956.00	22.43**
Site=Si	1	44534.00	202.49***	105740.00	70.10***
Time=Ti	5	7407.90	9.77***	9762.00	11.96***
Block=Bl(Si)	4	398.24	0.73	1508.60	2.15*
TrxBe	1	1110.40	5.05*	4012.50	3.92*
TrxTi	5	920.26	1.21	5758.00	9.46***
BexTi	5	9281.90	17.77***	11075.00	13.56***
TrxBl(Si)	4	219.93	0.41	1023.70	1.46
TixBl(Si)	20	758.16	1.40*	816.54	1.16
TrxBexTi	5	1313.20	2.51**	711.85	1.17
TrxTixBl(Si)	20	522.18	0.96	608.87	0.87
Residual	360	540.34		703.15	

Pairwise test						
		SW region			**PR region**	
	Time	Condition	P (MC)		Condition	P (MC)
TrxBexTi	T1	Levante x C vs R	**0.009**	TrxTi	C vs R	**0.0002**
		Cortadura x C vs R	**0.0077**			
	T3	Levante x C vs R	0.1103		C vs R	**0.0094**
		Cortadura x C vs R	0.8303			
	T6	Levante x C vs R	0.5265		C vs R	**0.0238**
		Cortadura x C vs R	0.3123			
	T16	Levante x C vs R	0.4613		C vs R	0.2019
		Cortadura x C vs R	0.9243			
	T32	Levante x C vs R	0.3778		C vs R	0.7199
		Cortadura x C vs R	0.3911			
	T47	Levante x C vs R	0.1551		C vs R	0.2023
		Cortadura x C vs R	0.3857			

DISCUSSION

In this study, we manipulated stranded organic debris in experimental areas located at the upper shores in order to evaluate the colonization patterns of supralittoral arthropods in wrack debris that had been naturally stranded in the successive tides. We investigated whether the colonization of natural wrack debris could cause a directional change in assemblages inhabiting the upper beach. According to our results, on the first three days after the stranding of new wrack debris, early (talitrids, isopods, and dipterans), middle, and late (tenebrionids, staphylinids, and spiders) taxonomical groups (according to Lavoie, 1985) were present in areas covered by naturally stranded wrack on beaches of both regions. Moreover, 7 and 4 taxa in PR region and SW region, respectively, of early, middle, and late stages were present in higher-abundance classes (i.e. between 2.0-2.5 to 3.0-3.5) in the recovered areas after 16 days, while an early stage taxon (i.e. talitrid amphipod) dominated these areas at the end of the experiment. Therefore, after a natural disturbance (i.e. the stranding of wrack) the colonization did not occur in a predictable pattern (*sensu* Lavoie, 1985), but instead species of different stages of succession colonized wrack debris stranded on the upper beaches. It is possible that the spatial and temporal heterogeneity created in areas recovered by naturally stranded wrack (i.e. wrack with different patch-sizes, degrees of dehydration, stages of decomposition, etc.) can offer a wide range of microhabitats and food sources, which lead to the presence of a wide range of colonizer species (i.e. early, middle, and late stages) in relation to their physiological tolerances (Lavoie, 1985) and their preference for specific microhabitats and/or food sources (Pennings et al., 2000; Rodil et al., 2008; Colombini et al., 2011; Ruiz-Delgado et al., 2015).

Previous studies have reported that algal wrack patches are rapidly colonized (within 3 days) by upper-shore arthropods (Inglis, 1989; Olabarria et al., 2007; Rodil et al., 2008; Dufour et al., 2012). Consistent with these assertions, multivariate analyses showed that the assemblages in recovered (i.e. manipulated) areas converged quickly (i.e. within a 3 day-period) with those in control areas on sandy beaches subsidized by algal wrack (in SW region). Notably, the colonization of mangrove-propagule debris (in the PR region) by supralittoral arthropods was slower (i.e. in 16-day period) after the natural stranding of wrack debris. A similar pattern was also reported for univariate descriptors of assemblages in the PR region. The total density was stabilized on 3 or 6 days (at Cem and Assenodi, respectively) after the stranding of wrack debris;

meanwhile, species richness and diversity reached similar values compared to the control areas on day 16. However, density, species richness, and diversity of assemblages associated with algal wrack (in the SW region) in recovered areas showed no consistent patterns of changes with respect to the control areas over time. Few studies have evaluated colonization patterns of supralittoral arthropods in accumulations of algal wrack debris that are naturally stranded by tides (Lavoie, 1985). Moreover, there are no available studies that have evaluated the colonization process in other types of wrack debris such as mangrove propagules on subtropical beaches. Therefore, the present study is the first report on the colonization by supralittoral arthropods after the stranding of both types of natural wrack debris (i.e. seaweed and mangrove propagules) on Atlantic sandy beaches.

The dynamics of wrack supply, as well as the different life-history attributes and behavioural strategies of species are offered as possible explanations of the colonization patterns detected in each Atlantic region. The availability of wrack debris is reported as the main factor structuring supralittoral communities (Ochieng and Erftemeijer, 1999; Dugan et al., 2003; Gonçalves and Marques, 2011). Therefore, the temporal variability of the wrack supply (i.e. wrack biomass) on the upper beach could determine the temporal changes in the colonizing communities of wrack debris at each region. In the PR region, the lower values of stranded biomass registered in the recovered areas with respect to the control areas during the first 6 days, especially on Assenodi beach, could determine the slowness (i.e. within a 16-day period) of the colonization process by supralittoral assemblages. This timing with recovered and control communities converged probably in coincidence with the time when the wrack biomass was also stabilized at each beach (i.e. day 6 at Cem and day 16 at Assenodi). However, in the SW region, the stranded biomass in the recovered plots quickly reached (within 3 or 6-days period) values similar to those of controls, apparently enabling the rapid colonization in the strandlines (within 3 days).

The temporal changes in the community structures after the stranding of wrack may be also explained by the different life-history attributes of species such as their colonizing and competitive abilities and the mobility of different taxa (e.g. Jaramillo et al., 2003; Olabarria et al., 2007) in each region studied. Moreover, species-specific strategies for exploiting wrack debris (as refuge and/or feeding site) may also lead to temporal changes in assemblages associated with wrack (Olabarria et al., 2007; Rodil et al., 2008) until reaching the control state. In Paraná region, *Platorchestia monodi* and

coleopterans (Tenebrionidae, Cleridae and Nitidulidae) showed unevenly increasing densities from the time of stranding wrack in recovered areas until reaching control levels. However, *P. monodi* showed a more protracted colonization pattern (i.e. a 16-day period) than did coleopterans (between 3 or 6 from the deposition of wrack debris). A possible explanation of these response patterns would be the mobility of these taxa. *P. monodi*, may have reduced mobility, as has been reported for others *beachhopper* species such as *Orchestia gammarellus* (Colombini et al., 2013), a situation that could explain that the colonization, through the movement of adults and juveniles was slow (i.e. within 16 days-period). This is a plausible explanation for the patterns of the coleopterans, but there are no studies available on the locomotory ability of these taxa. Another possible explanation could be the trophic habitats of these taxa. Analyses of the gut contents of *P. monodi* individuals indicated that this species feeds on micro-algae or bacteria (unpublished data). Therefore, it may not depend directly of wrack debris as a feeding site and, probably, this would probably influence its slow colonization pattern in recovered areas. However, Cleridae species are mainly carnivorous (Marinoni and Dutra, 1997) and presumably feed on larvae and immature individuals associated with wrack debris, while nitidulidae and tenebrionidae species are scavengers and may feed on decaying organic matter (Marinoni and Dutra, 1997; Colombini et al., 2011). Therefore, the availability of food sources in the recovered areas could influence colonization patterns. On the other hand, *Bledius bonariensis* initially showed a rapid colonization, with its abundance rising to significantly higher levels than controls, followed by a subsequent fall to control abundance values. This pattern was evident during a 6-day period, especially at Assenodi beach, when wrack biomass was very low in the recovered compared to control areas. Therefore, it is possible that *B. bonariensis* could be an opportunistic species. Its burrowing strategy and/or its feeding based on benthic microalgae (Herman, 1986) could promote an increase in its density on the supralittoral zone when the rest of the species showed low abundances. However, life-history attributes and behavioural adaptations of coleopterans inhabiting subtropical sandy beaches (such as Staphylinidae, Nitidulidae, Cleridae, etc.) are poorly understood, making it difficult to explain the response patterns of this taxonomic group.

On the other hand, in the SW Spain region**,** algal wrack patches were rapidly colonized (within 3 days) by upper-shore arthropods, mainly as a result of changes in Talitridae (i.e. *Talitrus saltator)*, which quickly recovered (within 3 days) after the stranding of the wrack. This could be driven by its great mobility (Scapini et al., 1992),

which could enable a rapid colonization of algal wrack through the movement of adults and juveniles from control areas or nearby areas where they could be hidden, due to its burrowing abilities (Wildish, 1988). Moreover, algal wrack is the main food source for *T. saltator* (Lastra et al., 2008; Olabarria et al., 2009; Colombini et al., 2011; Bessa et al., 2014), which could explain the rapid colonization of strandlines. On the other hand, Tenebrionidae (*Phaleria bimaculata* and larvae), Staphylinidae (*Phytosus spinifer*), and dipterans colonized wrack debris on days 1 and 3 after the stranding of wrack debris, although with lower values than the control areas. A rapid colonization of wrack debris for these taxa could be expected according to the results of previous studies on artificial algal patches (Olabarria et al., 2007; Garrido et al., 2008). However, no temporal trends can be inferred in the recovered areas during our experiment. It is possible that the highly dynamic conditions and quick changes in species density may necessitate a smaller temporal scale (e.g. hours) to analyse the temporal trends of these colonizer species in natural strandlines of the beaches studied.

The main outcome of the study was that naturally stranded wrack debris can be promptly invaded by a wide range of colonizer species (i.e. talitrid, dipterans, tenebrionids, staphylinids, and spiders) that indicate high heterogeneity of habitat and/or food sources available for supralittoral arthropods in natural driftlines. Moreover, the results show that the colonization of wrack debris resulted in detectable changes in the density of some taxa (such as talitrid amphipods, tenebrionids, and staphylinids), and, therefore, in the community structure, although the time to re-establish the structure of the associated assemblages varied in each region studied. The temporal variablity of wrack supply, the species-specific adaptations (i.e. mobility) and strategies to use wrack debris (as refuge and/or feeding site) appear to determine the different colonization patterns of supralittoral macroinvertebrates in natural strandlines on beaches of both Atlantic regions (Paraná and Spain). Although colonization patterns in natural strandlines is complex because several factors and processes might influence in colonizer species, this study represents the first report of the colonization process by supralittoral arthropods after the stranding of natural wrack debris on Atlantic upper shores.

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SUPPLEMENTARY MATERIAL

Table S1 Summary of seasonal climate data (temperature and precipitation, mean 1961-1990) of Paraná (PR) and Southwest of Spain (SW) regions. Physical characteristics of each surveyed beach include length and width, slope, Mz (mean sand grain size), T (wave period), Hb (wave height), Dean´s parameter, Tide (mean spring tide range), RTR (Relative Tide Range).

Region	**PR**		**SW**	
Autumm	June to August		October to December	
Temperature				
Seasonal mean (ºC)	18.00		16.83	
Precipitation				
Total season (mm)	271.90		276.40	
Beach	**Assenodi**	**Cem**	**Levante**	**Cortadura**
Beach length (m)	2100	1000	1000	2480
Intertidal width (m)	110	53	105	85
Slope (º)	1.26	2.40	2.03	2.19
Mz (mm)	0.27	0.23	0.18	0.23
T (s)	7.00	4.90	5.00	7.00
Hb (m)	1.00	0.25	0.35	0.65
Dean (Ω)	5.53	1.76	4.88	3.37
Tide (m)	1.70	1.70	2.00	2.00
RTR	1.70	6.80	5.71	3.08

Table S2 Total abundance (nº indv) and percent composition (% community) of arthropods found in the wrack deposits on beaches of Paraná region (Cem and Assenodi).

	Cem		Assenodi	
Taxa	Total abundance	% of community	Total abundance	% of community
Amphipoda				
Talitridae				
Platorchestia monodi	1283	53.10	771	37.00
Isopoda				
Tylidae				
Tylos niveus	1	0.04	1	0.05
Coleoptera				
sp1	5	0.20	9	0.43
larvae sp1	44	1.82	106	5.09
Tenebrionidae				
Phaleria testacea	149	6.17	2	0.10
Tenebrionidae larvae	51	2.11	1	0.05
Staphylinidae				
Bledius bonariensis	17	0.70	678	32.53
Bledius hermani	22	0.91	-	-
Bledius sp1	16	0.66	35	1.68
Bledius sp2	-	-	19	0.24
Gabronthus sp1	5	0.20	-	-
Heteroceridae				
Efflagitatus freudei	-	-	6	0.29
E. freudei larvae	-	-	50	2.40
Cleridae	300	12.41	31	1.49
Carabidae	-	-	280	13.44
Nitidulidae	394	16.30	55	2.64
Scarabeidae				
Aphodinae sp1	9	0.36	4	0.19
Curculionidae	2	0.08	-	-
Araneae				
Allocosa brasiliensis	9	0.37	20	0.96
Araneae sp1	19	0.78	8	0.39
Araneae sp2	6	0.25	-	-
Araneae sp3	-	-	3	0.14
Araneae sp4	-	-	-	-
Araneae sp5	1	0.04	-	-
Diptera	83	3.44	19	0.91
Total abundance	2416		2098	
Total number of species	19		17	

Table S3 Total abundance (nº indv) and percent composition (% community) of arthropods found in the wrack deposits on beaches of SW of Spain region (Levante and Cortadura).

	Levante		Cortadura	
Taxa	Total abundance	% of community	Total abundance	% of community
Amphipoda				
Talitridae				
Talitrus saltator	813	48.25	4569	74.23
Isopoda				
Armadillidae				
Armadillium sp1	4	0.24	-	-
Tylidae				
Tylos europaeus	-	-	40	0.65
Coleoptera				
Tenebrionidae				
Phaleria bimaculata	33	1.96	37	0.60
Tenebrionidae larvae	69	4.09	125	2.03
Staphylinidae				
Myrmecopora sulcata	1	0.06	2	0.03
Hydrosmecta thinobioides	7	0.42	-	-
Tachyporus pusillus	1	0.06	1	0.02
Aleochara bipustulata	1	0.18	-	-
Acrotona orbata	17	1.00	17	0.27
Aloconota gregaria	27	1.60	14	0.22
Phytosus spinifer	52	3.09	571	9.27
Carpelimus rivularis	13	0.77	8	0.13
Anotylus nitidulus	24	1.42	6	0.10
Remus sericeus	2	0.12	12	0.19
Cafius xantholoma	11	0.65	14	0.23
Curculionidae	7	0.42	6	0.11
Carabidae	15	0.89	5	0.09
Chrysomelidae	8	0.47	1	0.02
Elateroidae	2	0.12	-	-
Scarabidae	3	0.18	-	-
Histeridae	8	0.47	6	0.11
Araneae				
Lyniphiidae	37	2.20	9	0.16
Agelinidae	1	0.06	-	-
Salticidae	2	0.12	-	-
Diptera				
Adults	276	16.38	49	0.89
Larvae sp1	153	9.08	9	0.16
Pupae sp1	24	1.42	5	0.09
Himenoptera				
Pteromalidae	15	0.89	-	-

Table S3 Continued

	Levante		Cortadura	
Taxa	Total abundance	% of community	Total abundance	% of community
Hemiptera				
Psylloidea	39	2.31	2	0.04
Saldidae				
Saldula saltoria	15	0.89	-	-
Thysanoptera	2	0.12	-	-
Total abundance	1685		5508	
Total number of species	29		20	

Table S4 SIMPER (Similarity Percentage) analysis listing species that contribute collectively to at least 70% of total assemblage dissimilarity between treatments (control and recovered) at the sampling times. Ten larvae-Tenebrionidae larvae Codes for higher Taxa: AMP: Amphipods, COL: Coleopterans.

a) PR region

T1

Species		**Recovered**	**Control**		
90.19% dissimilarity		Av.Abund	Av.Abund	Contrib%	Cum.%
P. monodi	AMP	0.03	1.38	35.53	35.53
B. bonariensis	COL	0.59	0.46	21.05	57.09
Nitidulidae	COL	0.00	0.85	20.07	77.16
Cleridae	COL	0.06	0.39	9.42	83.19
P. testacea	COL	0.00	0.36	6.43	93.01

T3

Species		**Recovered**	**Control**		
60.01% dissimilarity		Av.Abund	Av.Abund	Contrib%	Cum.%
P. monodi	AMP	0.69	1.44	26.99	26.99
B. bonariensis	COL	0.99	0.80	24.69	51.68
Nitidulidae	COL	0.45	0.82	17.71	69.38
Cleridae	COL	0.32	0.52	12.38	81.76
P. testacea	COL	0.28	0.35	9.93	91.69

T6

68.48% dissimilarity		Av.Abund	Av.Abund	Contrib%	Cum.%
P. monodi	AMP	0.56	1.17	28.33	28.33
B. bonariensis	COL	0.72	0.44	25.80	54.14
Nitidulidae	COL	0.42	0.64	19.27	73.41
Cleridae	COL	0.34	0.43	13.69	87.09
P. testacea	COL	0.09	0.24	7.21	94.30

T16

66.85% dissimilarity		Av.Abund	Av.Abund	Contrib%	Cum.%
P. monodi	AMP	0.98	1.27	31.37	31.37
B. bonariensis	COL	0.37	0.21	20.45	51.83
Cleridae	COL	0.39	0.51	19.18	71.01
Nitidulidae	COL	0.32	0.31	14.94	85.95
P. testacea	COL	0.24	0.13	7.54	93.49

b) SW region

T1-Levante

Species		**Recovered**	**Control**		
53.58% dissimilarity		Av.Abund	Av.Abund	Contrib%	Cum.%
T. saltator	AMP	0.98	1.69	43.18	43.18
Ten larvae	COL	0.53	0.00	22.69	65.88
Diptera	DIP	0.18	0.17	10.89	76.76
P. bimaculata	COL	0.25	0.00	9.10	85.86

T1-Cortadura

Species		**Recovered**	**Control**		
44.32% dissimilarity		Av.Abund	Av.Abund	Contrib%	Cum.%
T. saltator	AMP	1.49	2.12	39.51	39.51
Ten larvae	COL	0.22	0.62	22.05	61.57
P. spinifer	COL	0.21	0.56	19.29	80.86
Diptera	DIP	0.11	0.33	13.16	94.02

Tabla S4 Continued

b) SW region

T3-Levante		**Recovered**	**Control**			**T3-Cortadura**		**Recovered**	**Control**		
51.95% dissimilarity		Av.Abund	Av.Abund	Contrib%	Cum.%	44.32% dissimilarity		Av.Abund	Av.Abund	Contrib%	Cum.%
Diptera	DIP	0.54	1.23	28.34	28.34	*T. saltator*	AMP	2.26	2.46	42.17	42.17
T. saltator	AMP	0.76	0.82	22.73	51.07	Diptera	DIP	0.28	0.17	17.42	59.59
Ten larvae	COL	0.59	0.65	18.09	69.16	*P. spinifer*	COL	0.17	0.19	13.71	73.30
P. bimaculata	COL	0.12	0.32	9.28	78.44						
P. spinifer	COL	0.06	0.22	7.10	85.54						

ARE STRANDLINE MACROFAUNAL ASSEMBLAGES AFFECTED BY WRACK REMOVAL ACTIVITY? AN EXPERIMENTAL APPROACH ON ATLANTIC SANDY BEACHES OF SPAIN AND BRAZIL

Are strandline macrofaunal assemblages affected by wrack removal activity? An experimental approach on Atlantic sandy beaches of Brazil and Spain

ABSTRACT

Because beaches should be attractive to the tourist, improving their aesthetic appeal by removing wrack debris at the drift-lines is a common practice on sandy beaches worldwide. However, wrack is used as shelter or breeding sites, and/or as food source for supralittoral arthropod assemblages. In this study, we performed an experimental design (M-BACI), for the first time, to assess the direct effects of wrack removal on macroinvertebrates associated with wrack debris from beaches located on both sides of the Atlantic Ocean (southern Brazil and south-western Spain). We hypothesised that, regardless of species differences, the reduction of wrack availability would reduce the total density and species richness and could change the overall structure of assemblages associated with wrack debris. The significant reduction of wrack biomass after the removal activity corresponded to changes in supralittoral arthropod assemblages over the short-term (between 3 to 16 days) in the Paraná region (southern of Brazil). These changes were attributed to declines in the total density of the amphipod *Platorchestia monodi* and the coleopterans Cleridae and Nitidulidae followed by a quick recovery in disturbed areas after the wrack removal. On the other hand, temporal differences were detected on beaches from south-western Spain region regarding the reduction of total density of the amphipod *Talitrus saltator* within the first three days after the disturbance. The temporal variability of wrack supply and the species-specific behavioural strategies could influence the recovery patterns of assemblages inhabiting the strandlines of the upper shores in both regions. This study provides fundamental quantitative information about the effects of wrack removal on strandline-associated macroinvertebrates in Atlantic sandy beaches.

Keywords: disturbance, wrack, arthropods, community, supralittoral, beaches, Atlantic coast.

INTRODUCTION

A distinctive feature of exposed sandy beaches is their low *in situ* primary productivity, and thus beach food webs depend largely upon allochthonous organic debris from the sea and coastal areas (Griffiths et al., 1983; Colombini and Chelazzi, 2003; Dugan et al., 2003). These organic debris (called wrack) usually accumulates at the highest water level along the upper shores forming the strandlines. On sandy shores with high amounts of wrack, upper-shore macroinvertebrates (mainly crustaceans and isopods) tend to concentrate in the supralittoral zone and even become restricted to the strandlines (Gonçalves and Marques, 2011; Bessa et al., 2014a). Moreover, previous studies have reported the strong association of supralittoral macroinvertebrate assemblages with wrack deposits, showing higher abundances and numbers of species in wrack-covered areas than in bare-sand areas (Dugan et al., 2003; Jaramillo et al., 2006; Ince et al., 2007; MacMillan and Quijón, 2012; Ruiz-Delgado et al., 2015). Strandlines are patchy and ephemeral, and therefore, their spatial and temporal variability influence the distribution and zonation of invertebrate assemblages on the upper shores (Stenton-Dozey and Griffiths, 1983; Dugan et al., 2003; Gonçalves and Marques, 2011).

Strandlines are composed of several types of organic materials (Colombini and Chelazzi, 2003). Marine macrophytes and macroalgae from offshore seaweed beds are common components in sandy beaches from temperate regions (Jędrzejczak 2002a; Ince et al., 2007; Lastra et al., 2008; Barreiro et al., 2011; Colombini et al., 2011a), while propagules, fruits, and leaves from the mangroves are one of the major organic components of driftlines on tropical and subtropical sandy beaches (Colombini and Chelazzi, 2003; Ruiz-Delgado et al., 2014). These inputs support abundant and diverse macrofaunal communities, dominated by terrestrial invertebrates such as talitrids, staphylinids, and tenebrionids which use this debris for shelter or breeding, and/or as a food source (Ruiz-Delgado et al., 2014). Since many of these organisms act as linkage between organic inputs and higher trophic consumers (Brown and McLachlan, 2002; Dugan et al., 2003; McLachlan and Brown, 2006), the availability of wrack to support their abundance and biomass is an important factor to maintain the diversity and abundance as well as the energy flows between marine and terrestrial ecosystems (Polis and Hurd, 1996; Spiller et al., 2010; Mellbrand et al., 2011).

Sandy beaches are iconic assets, culturally and socio-economically valuable to coastal societies (Defeo et al., 2009; Schlacher et al., 2014). Beaches are typically viewed as natural places of "sun, sea, surf, and sand" that support many leisure activities (Davenport and Davenport, 2006). On the other hand, beaches are also ecosystems that provide many services and have great ecological value (Defeo et al., 2009). However, beach management in sandy beaches worldwide concentrates largely on providing recreational uses. Because beaches should be attractive to the tourists, improving the aesthetic appeal by removing organic materials at the driftlines is a common practice in sandy beaches (Davenport and Davenport, 2006; Schlacher et al., 2008; Defeo et al. 2009; McLachlan et al., 2013). Nevertheless, previous studies have indicated that the removal of wrack may be ecologically damaging by disrupting pathways of decomposition and nutrient exchange between marine and terrestrial ecosystems as well as by altering the composition of upper-shore invertebrate communities and prey availability to higher trophic levels, such as shorebirds, lizards, and rodents (e.g. Llewellyn and Shackley, 1996; Kirkman and Kendrick, 1997; Dugan et al., 2003; Fairweather and Henry, 2003; Martin et al., 2006; Spiller et al., 2010; Dugan et al. 2011; Barreiro et al. 2013; Gilburn, 2012; Lafferty et al., 2013).

Until now, the effects of wrack removal have been evaluated as a disturbance associated with beach grooming (Llewellyn and Shackley, 1996; Dugan et al., 2003; Gilburn, 2012). However, these studies used "compare and contrast" designs in which the putative effects of the wrack removal on macroinvertebrate assemblages can be confounded with those associated with mechanical cleaning (i.e. removal of sand, crushing of organisms, redistribution of animals, deeper burial, etc.) and other potential anthropogenic impacts such as trampling, recreational activities or habitat modification (e.g. artificial structures), which may disturb beach macroinvertebrates (e.g. Fanini et al., 2005; Colombini et al., 2011b; Schlacher and Thompson, 2012; Bessa et al., 2014b). No experimental study available has isolated this source of disturbance (i.e. wrack removal) to assess its direct effects on strandline-associated fauna. This assessment highlights the impact that only the removal of wrack debris could have on strandline arthropods. Consequently, in the present study, we conducted a field experiment to investigate the short-term effects of wrack removal on macroinvertebrate assemblages associated with wrack debris on natural and ungroomed upper shores. We hypothesised that the temporary removal of strandlines would reduce the total density and species richness and could change the overall structure of assemblages associated

with wrack debris. Given that wrack debris are removed from sandy beaches worldwide, studies in different regions of the world are needed in order to understand the effects of this disturbance in other regions and to assess its global impact. Hence, this study was performed on sandy beaches located on both sides of the Atlantic Ocean (southern Brazil and south-western Spain) to assess whether, irrespective of species differences, the reduction of wrack availability involves similar response patterns in the structure of the communities associated with wrack debris. This assessment should be considered an initial step towards a more comprehensive and robust evaluation of potential effects of the removal of a key component (i.e. organic debris) on beach ecosystem functioning.

MATERIALS AND METHODS

Study area

This study was conducted on four sandy beaches located in two geographical regions (Fig. 1): South of Brazil (Paraná-PR) and Southwest of Spain (SW Spain). Regardless of its geographic locations and morphodynamic states, all beaches have natural and ungroomed backshores and receive continuous allochthonous inputs deposited in the supralittoral zone.

In the Paraná coast two sandy beaches were selected (Cem and Assenodi) located near the Paranaguá estuary (Fig. 1). This coastal region presents a humid subtropical climate and semidiurnal tides with maximum amplitude of about 2 m (Knoppers et al., 1987). Cem (25º 34´24´´S; 48º 20´13´´W) is a low-energy reflective beach, modified by tides. It is a narrow beach (width approximately 53 m) characterized by fine sands (mean grain size = 0.23 mm) and a gentle slope (2.4º). Assenodi (25º 35´24´´S; 42º 22´04´´W) is an intermediate to dissipative, wave-dominated beach with fine sands (mean grain size = 0.27 mm), gentle slope (1.26º) and~110 m in width. Both beaches are bordered by *restinga* (i.e. coastal sand dune vegetation). Wrack deposits of these studied beaches were composed of three types of mangrove propagules: *Laguncularia racemosa* (23%), *Rhizophora mangle* (21%) and *Avicennia schaueriana* (15%) as well as by terrestrial-derived vegetation (40%).

In the Atlantic coast of Cadiz (SW Spain) two sandy beaches were selected (Levante and Cortadura). This coastal region is characterized by a dry-summer subtropical climate and semidiurnal tidal regime with a range between 3.2 and 1.1 m (Benavente et al., 2002). Levante (36º 33´37´´N; 6º 13´27´´W) located in the outer zone

of Cadiz Bay, is a dune-backed, wave-dominated, and dissipative beach. It is a wide beach (width approximately 100 m) characterized by fine-sized sand (mean grain size = 0.18 mm) and gentle slope (2.03º). Cortadura (36º28'58''N; 6º15'77''W), located at south of the Cadiz Bay, is a wave-dominated, and intermediate beach. It is backed by foredunes and low vegetated dune ridges, with fine-sized sand (mean grain size = 0.23 mm), gentle slope (2.19º), and~85 m in width. The driftlines of Levante were composed of two seagrass species: *Zostera noltei* (60%) and *Cymodocea nodosa* (40%). Meanwhile at Cortadura wrack deposits were composed by a mixture of brown macroalgae (66%) such as *Dictyopteris membranacea* and *Cladostephus spongiosus*, several species of red algae (29%) such as *Halopithys incurva* and *Chondria dasyphylla* and green algae (5%) such as *Codium decorticatum* and *Codium fragile.*

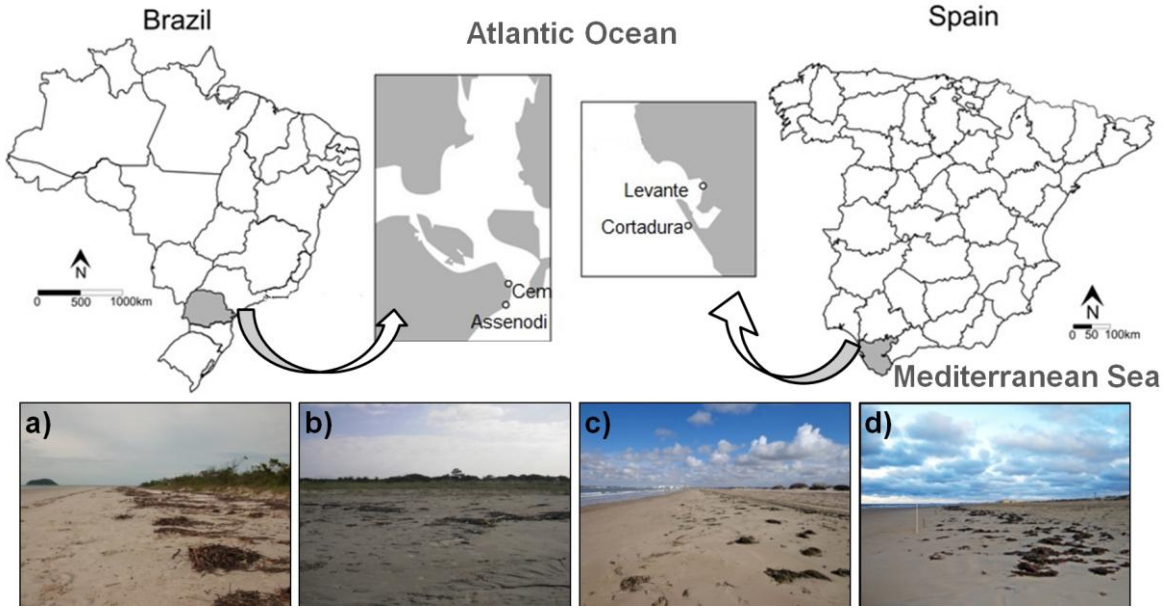

Figure 1. Geographic location of the study site on the southern coast of Brazil and the southwest coast of Spain, showing the four sandy beaches sampled: Cem (a) and Assenodi (b) (PR region); Levante (c) and Cortadura (d) (SW region).

Study design and sampling methods

A field experiment was performed between 24 May and 4 July 2012 in the PR region and 2 October and 12 November 2012 in SW region to evaluate the effects of wrack removal on upper shores assemblages. The M-BACI (multiple before-and-after control-impact) sampling design was used for analysing the possible effects of this planned disturbance. This is a robust methodology includes multiple control and impacted

locations which are compared in multiple sampling dates within before (baseline samples) and after start-up the impacting activity. The underlying assumption in this approach is that the impacted locations would have behaved approximately the same as the control locations in the absence of the disturbance (Underwood 1994; Keough and Mapstone 1997; Downes et al., 2004). In this study, a disturbance could inferred if changes at the impacted locations differed from those at the control locations, due to the impacted locations depart from 'normal' behaviour (Downes et al., 2004).

The experimental design included six plots, three control (C) and three impacted (I), each 15 m wide, delimited in an area of 115 m long extending from the base of the dune to the driftline on each beach. We used an interspersed design (*sensu* Hurlbert, 1984) in which the first plot along the shore on each beach was randomly assigned to a treatment (impacted and control), and treatments were assigned to the remaining plots in an alternating manner. Plots were spaced 5 m apart. Biological responses between control and impacted plots were monitored in pre-established temporal scales: before (-16, -6, -3 and -1 days) and after (+1, +3, +6 and +16 days) the 10-days experimental removal (Fig. 2). Samplings were performed during low tides, when MHWS (mean high water springs) varied between 1.4-1.6 m on PR region and 1.2-1.5 m on SW Spain region and wrack debris were stranded on the current high-tide line of the beaches studied (see Ruiz-Delgado et al., 2014). Wrack debris that accumulated into impacted plots were raked and removed with the aid of garden rakes. Moreover, wrack was also removed from the spacing among plots (5m) and the intertidal zone. The wrack removal was carried out for 10 consecutive days (between -1 and +1 days; Fig 2) to ensure a significant reduction of wrack biomass and, therefore, a change in the community structure at the strandlines. On the other hand, the control plots remained with wrack deposits and represented the undisturbed condition.

Wrack coverage was measured from photographs taken within six 1x1 m quadrats placed randomly in each treatment plot (control and impacted) during each sampling date (i.e. 144 photographs per treatment). Moreover, at each plot, random samples (n=6) were collected pushing a core (15 cm in diameter and 20 cm in depth) vertically through the wrack mat into the sediment to collect wrack debris as well as associated fauna and macrofauna underneath the wrack debris. Samples were taken within each photographed quadrat. At the free end of the core, a plastic bag was used to prevent mobile fauna (mainly insects and amphipods) from escaping. Samples were transferred into 70% ethanol to the laboratory to be washed and sieved through a 0.5

mm mesh. The macroinvertebrates retained were sorted and identified to the highest possible taxonomic separation. Species number, density (expressed as total number of ind.m^{-2} of the surface covered by wrack deposits), and diversity (Shannon-Wiener index) were calculated for each sample. All wrack debris was separated and dried to a constant weight at 60ºC (g dw). The coverage was estimated as the percentage of plot surface (1x1 m quadrat) covered by wrack debris using Image J (v. 1.45) (Abràmoff et al., 2004). For an estimate of the amount of stranded wrack in each plot (g dw/m^2), the values of wrack biomass per core and the coverage of each sampling date were used.

Data analysis

Differences in wrack biomass and univariate descriptors (total density, species richness and Shannon-Wiener´s index) were tested using a 4-way analysis of variance, which included the following factors (Fig. 2): period (Pe, 2 levels: before and after impact, fixed and orthogonal), sampling time (Ti, 4 levels, fixed and nested within each period), treatment (Tr, 2 levels: control and impact, fixed and orthogonal), and plot (Pl, 3 levels, random and nested in each treatment). In this design, the effect of wrack removal on macrofaunal assemblages was identifiable as interactions between treatment and period or as differences among treatments at any particular time after the experimental wrack removal on each studied beach. Homogeneity of variance was examined by Cochran's test and normality was analysed through visual inspection of residual and probability plots. Data were transformed if variances were significantly different at p=0.05. For non-homogeneous variances, ANOVA was, nevertheless, used after setting p=0.01, to reduce the chance of Type I error (Underwood, 1997). Significant effects and interactions were further investigated through multiple comparisons using Student–Newman–Keuls's (SNK) tests (p=0.05).

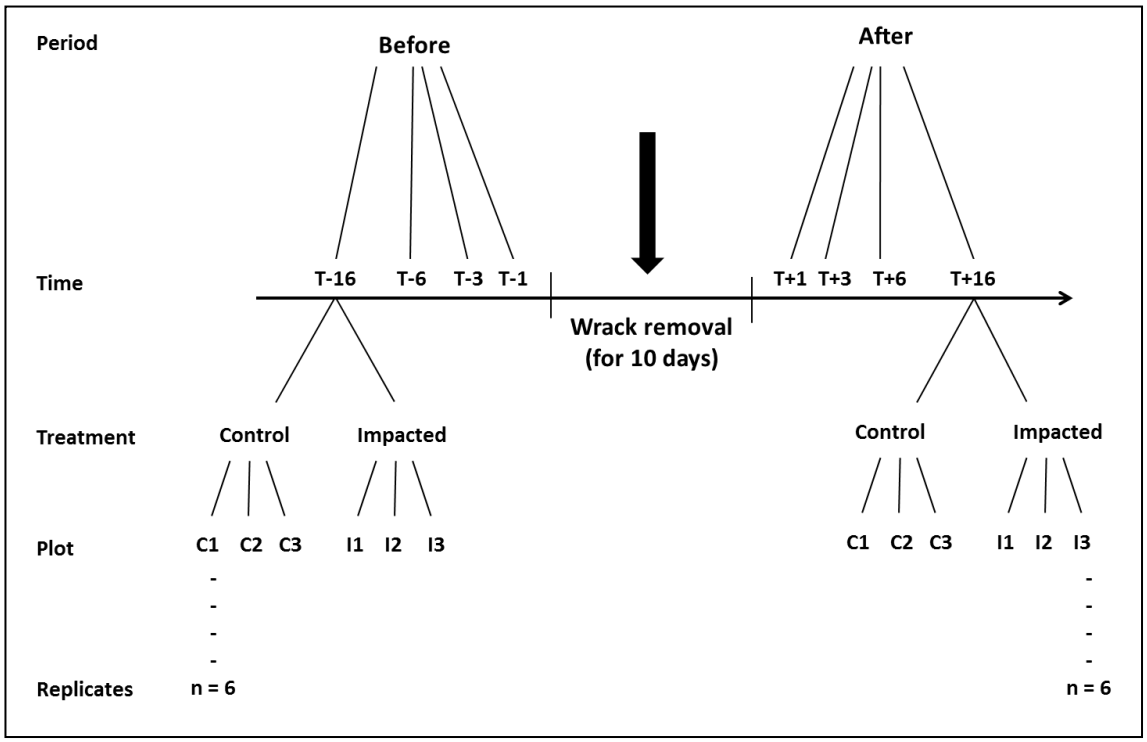

Figure 2.M-BACI design used in the field experiment and the data analysis. T =Time (days); I (impacted) and C (control) plots; n=numbers of samples in each plot and at each sampling date.

A permutational multivariate ANOVA (PERMANOVA, Anderson, 2001) based on the same design used for the univariate analyses was performed to test the hypothesis on differences in structure of macroinvertebrate assemblages between treatments after the wrack removal during the field experiment. Only significant effects ($p<0.05$) were further investigated through a series of *a posteriori* pair-wise comparisons. All taxa that occurred in less than 10% of the samples (out of a total of 288 samples) were excluded from the analysis, to reduce the number of zeros in the data matrix. The similarity matrices were calculated using the Bray–Curtis coefficient based on fourth-root transformed data. The statistical significant of variance components were tested using 9999 permutations and a significance level $\alpha=0.05$; whether the number of possible permutations were lower than 150, the Monte Carlo p-value (p (MC)) was used. To gauge the contribution of individual species to overall dissimilarity in community structure between treatments and times SIMPER analysis was used. Non-parametric multidimensional scaling (MDS), based on distance of dissimilarity matrix, was used to visualize the temporal trajectory of the assemblage structure between treatments on studied beaches from each region (Clarke and Warwick, 1994). Univariate analyses

were performed using the GAD package (Sandrini-Neto and Camargo, 2013) in R 2.15.2 (R Development Core Team, 2012) and multivariate analyses were carried out using the PRIMER v.6 with the PERMANOVA+ add on (PRIMER-E Ltd., Plymouth, UK).

RESULTS

Wrack biomass

The removal of wrack debris involved variations in the stranded wrack biomass between treatments, although the temporal pattern was different on beaches of each region studied. On sandy beaches of the Paraná region, the wrack biomass varied significantly between treatments from one time to another within each period (i.e. significant Tr×Ti(Pe) interaction, Table 1). Immediately after the impact, the wrack biomass was significantly lower in the impacted than control plots at both beaches (SNK tests $p<0.001$; Fig. 3). The amount of wrack was comparable between treatments on day 3 at Cem (Fig 3), while at Assenodi it continued to vary between treatments with lower values in the impacted plots with respect to the control plots until the end of the experiment (SNK tests $p<0.001$; Fig. 3). On sandy beaches from SW region, the Tr×Ti(Pe) interaction for wrack biomass also proved significant (Table 1). One day after the disturbance, the mean of wrack biomass was significantly lower in the impacted plots than in controls (SNK test $p<0.001$; Fig. 3), while three days later, no differences were detected between the treatments at Cortadura beach (SNK test $p>0.05$; Fig. 3); meanwhile the wrack biomass remained significantly lower in the impacted than in the control plots until six days after the disturbance at Levante beach (SNK test $p<0.001$; Fig. 3).

Wrack-associated fauna contrasts

Removal of wrack involved a temporary reduction in wrack availability corresponded with temporal variation in supralittoral arthropods assemblages. However, this effect seems significant in PR region compared to SW region. In PR region**,** impacted areas showed lower density of individuals associated with wrack debris compared with controls areas one day after the wrack removal (about -48% reduction at Assenodi, Fig. 4a; -110% to -79% reduction at Cem, Fig. 4d). Nevertheless, these differences were only significant at Cem beach (SNK test $p<0.001$; Tr×Ti(Pe), Table 1). At this beach,

density were comparable between both treatments on day 3 (SNK test, $p>0.05$). The number of taxa and diversity (Shannon-Wiener index) were also lower in impacted than in control plots on day 1 (richness: -90% to -77% reduction at Cem and about -55% reduction at Assenodi, Fig. 4 b,e; diversity: about -60% and 86% reduction at Assenodi and Cem respectively; Fig. 4c,f), but significant differences between treatments was only detected for diversity at Cem beach (SNK test, $p<0.001$; Tr×Ti(Pe), Table 1). In SW region, the removal of wrack debris at the upper shores not matched the temporal patterns of the univariate community descriptors detected at PR region. Density, species richness and diversity were comparable between treatments at both Levante and Cortadura beach (Fig. 5; Table 1).

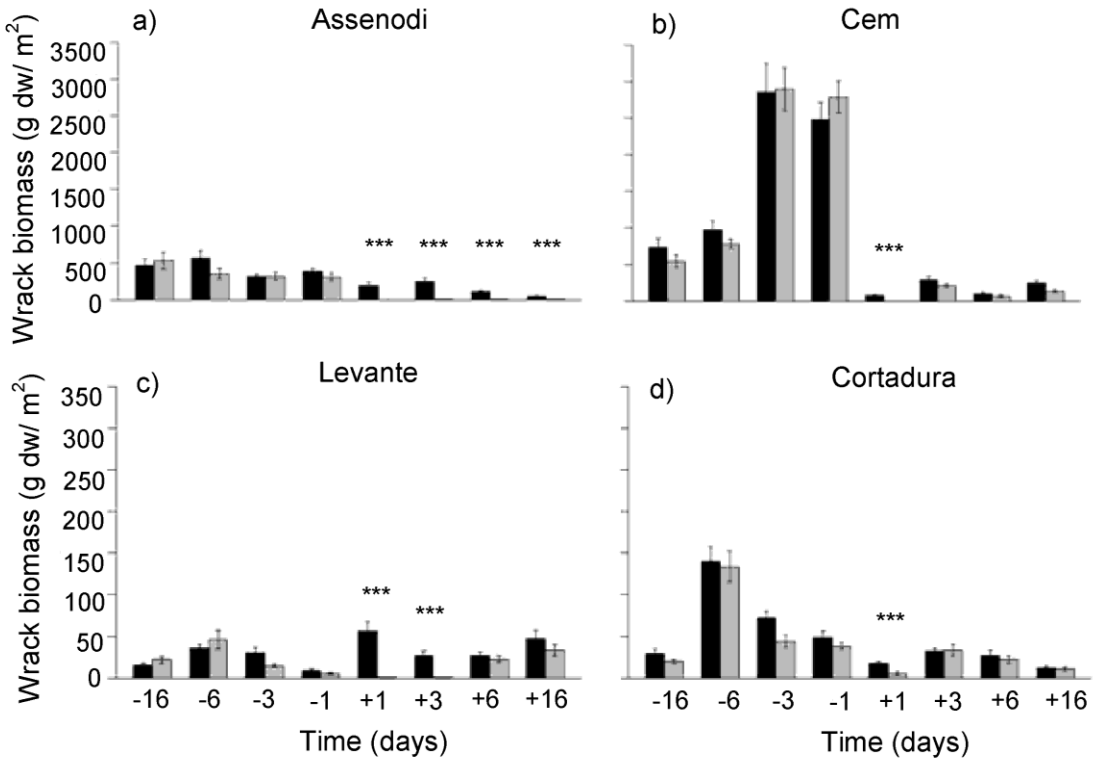

Figure 3. Spatial-temporal changes in wrack biomass (g dw/m²) before (-16, -6, -3, -1 days) and after (+ 1, +3, +6, +16 days) wrack removal in the control (black column) and impacted (gray column) treatments at Assenodi, Cem (PR region), Levante, and Cortadura (SW region) beaches. Data are mean of wrack biomass ± S.E. (n=18, average of treatment plots). Significative differences between treatments (control and impacted) after the impact at any time was also represented (SNK tests, *** $p<0.001$).

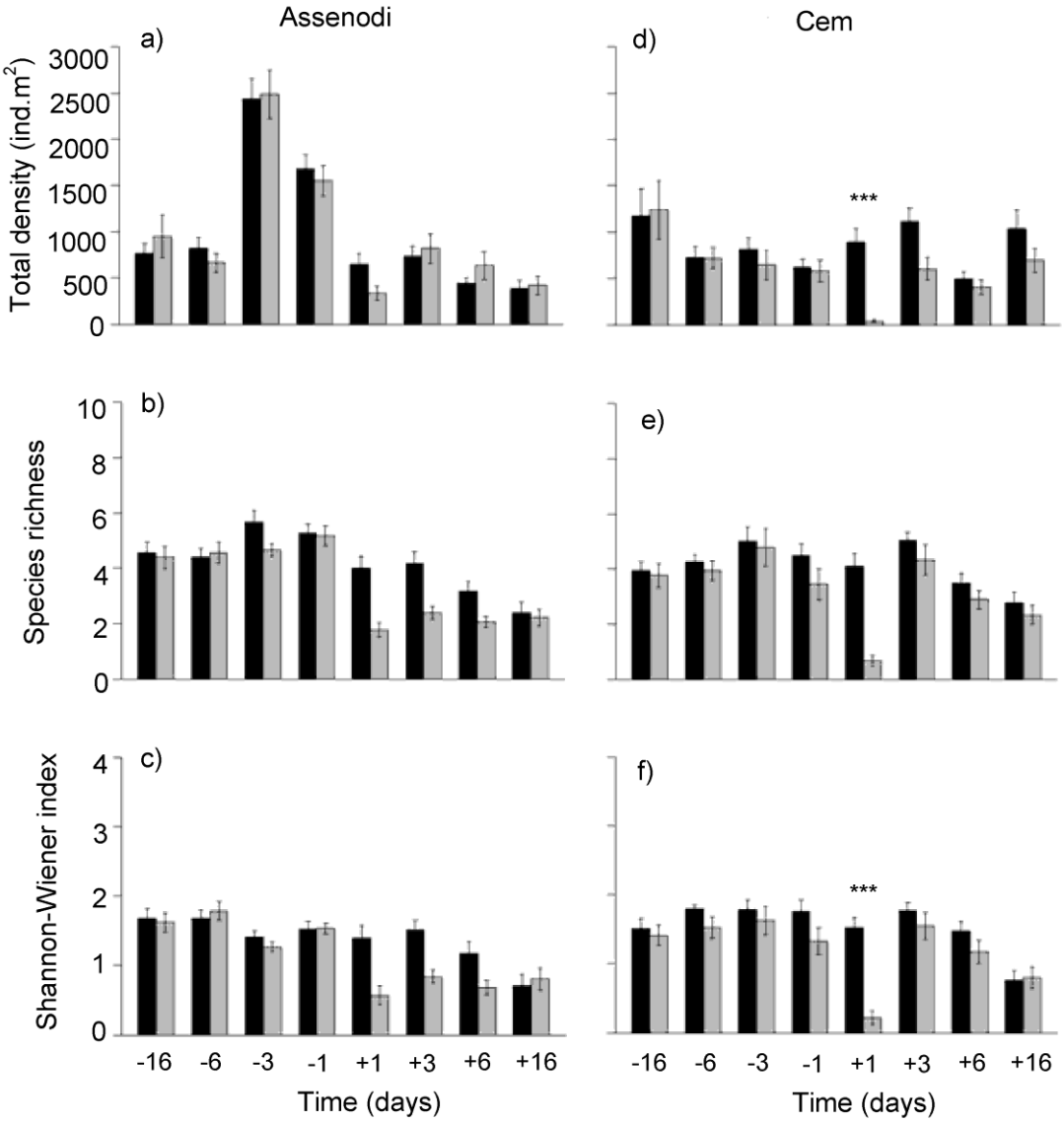

Figure 4. Spatial-temporal changes in total density (a, d), species richness (b, e) and diversity index (c, f) before (-16, -6, -3, -1 days) and after (+ 1, +3, +6, +16 days) wrack removal in the control (black column) and impacted (gray column) treatments at Assenodi and Cem beaches (PR region). Mean values ± S.E. (n=18, average of within each treatment) are represented. Significative differences between treatments (control and impacted) at any time was also represented (SNK tests, *** $p<0.001$).

Table 1 Summary of the ANOVAs for the M-BACI model for wrack biomass (a) and community descriptors [total density (b), species richness (c) and diversity index (d)] from the two Brazilian beaches (Assenodi and Cem) and the two Spanish beaches (Levante and Cortadura). Significant terms of interest (p= 0.05) are highlighted in bold.

		Assenodi beach			**Cem beach**			**Levante beach**			**Cortadura beach**		
Source	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
(a) Wrack biomass													
Treatment = Tr	1	106.90	11.78	0.026	13.60	43.29	0.003	17.69	26.66	0.007	4.75	18.06	0.013
Period = Pe	1	361.50	77.52	< 0.001	710.41	790.66	< 0.001	0.09	0.47	0.538	48.06	269.48	< 0.001
Plot = Pl(Tr)	4	9.60	23.13	< 0.001	0.31	0.678	0.608	0.66	3.91	0.004	0.26	1.08	0.364
Time = Ti(Pe)	6	2.40	6.68	< 0.001	43.93	48.81	< 0.001	6.85	19.38	< 0.001	7.24	25.16	< 0.001
Tr * Pe	1	69.65	14.95	**0.018**	10.58	11.78	**0.027**	11.77	57.06	**0.002**	0.35	1.98	0.232
Tr * Ti(Pe)	6	1.78	4.96	**0.002**	4.56	5.07	**0.002**	3.66	10.38	**< 0.001**	1.22	4.23	**0.004**
Pl(Tr) * Pe	4	4.66	13.00	< 0.001	0.90	1.00	0.428	0.21	0.58	0.677	0.18	0.62	0.652
Pl(Tr) * Ti(Pe)	24	0.36	0.92	0.58	0.90	1.94	0.007	0.35	2.08	0.003	0.29	1.18	0.256
Residuals	240	0.39			0.46			0.17			0.24		
Transformation		(4th root)			(4th root)			(4th root)			(4th root)		
(b) Total density													
Treatment = Tr	1	2.31	0.75	0.437	61.05	11.13	0.029	5.70	13.96	0.002	10.08	2.57	0.184
Period = Pe	1	137.52	39.61	0.003	22.00	7.55	0.051	0.52	0.18	0.693	421.54	54.32	0.002
Plot = Pl(Tr)	4	3.09	3.38	0.010	5.49	2.48	0.045	0.41	0.16	0.960	3.93	1.19	0.315
Time = Ti(Pe)	6	18.24	10.59	< 0.001	14.22	3.92	0.007	15.04	5.23	0.001	101.44	12.87	< 0.001
Tr * Pe	1	0.20	0.06	0.822	23.79	8.17	**0.046**	0.01	0.00	0.961	7.25	0.93	0.388
Tr * Ti(Pe)	6	1.87	1.09	0.398	10.35	2.85	**0.031**	3.38	1.18	0.352	6.59	0.84	0.554
Pl(Tr) * Pe	4	3.47	2.02	0.124	2.91	0.80	0.535	2.86	1.00	0.428	7.76	0.98	0.435
Pl(Tr) * Ti(Pe)	24	1.72	1.88	0.009	3.63	1.64	0.034	2.87	1.10	0.343	7.88	2.39	< 0.001
Residuals	240	0.92			2.22			2.61			3.30		
Transformation		(4th root)			(4th root)			log(x+1)			(4th root)		

Table 1 Continued

		Assenodi beach			Cem beach			Levante beach			Cortadura beach		
Source	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
(c) Species richness													
Treatment = Tr	1	45.92	26.14	0.007	55.13	5.85	0.073	0.06	2.32	0.202	0.46	4.80	0.094
Period = Pe	1	306.28	70.68	0.001	72.00	22.91	0.009	0.67	14.83	0.018	0.48	1.36	0.308
Plot = Pl(Tr)	4	1.76	0.84	0.500	9.43	3.21	0.014	0.03	0.22	0.924	0.10	0.52	0.723
Time = Ti(Pe)	6	6.22	2.37	0.062	23.73	4.74	0.003	0.57	5.20	0.001	5.48	25.38	< 0.001
Tr * Pe	1	19.53	4.51	0.101	13.35	4.25	0.108	0.03	0.72	0.443	0.68	1.93	0.238
Tr * Ti(Pe)	6	4.74	1.80	0.141	9.98	2.00	0.106	0.12	1.09	0.398	0.43	2.01	0.104
Pl(Tr) * Pe	4	4.33	1.65	0.195	3.14	0.63	0.647	0.05	0.41	0.780	0.35	1.64	0.198
Pl(Tr) * Ti(Pe)	24	2.63	1.26	0.193	5.01	1.71	0.024	0.11	0.93	0.564	0.22	1.18	0.265
Residuals	240	2.09			2.94			0.12			0.18		
Transformation		none			none			(2th root)			(2th root)		
(d) Diversity													
Treatment = Tr	1	4.45	38.37	0.003	8.36	6.92	0.058	0.02	0.25	0.646	0.10	0.18	0.695
Period = Pe	1	26.24	38.51	0.003	13.53	19.10	0.012	5.25	34.07	0.004	5.28	23.00	0.009
Plot = Pl(Tr)	4	0.12	0.40	0.807	1.21	3.04	0.018	0.09	0.22	0.926	0.56	2.68	0.032
Time = Ti(Pe)	6	1.07	2.56	0.046	3.28	5.69	< 0.001	3.68	8.70	< 0.001	3.04	9.67	< 0.001
Tr * Pe	1	3.66	5.37	0.081	0.75	1.06	0.361	0.01	0.03	0.868	0.79	3.44	0.137
Tr * Ti(Pe)	6	0.78	1.85	0.132	1.66	2.88	**0.030**	1.05	2.50	0.052	0.21	0.67	0.673
Pl(Tr) * Pe	4	0.68	1.63	0.200	0.71	1.23	0.326	0.15	0.36	0.832	0.23	0.73	0.581
Pl(Tr) * Ti(Pe)	24	0.42	1.46	0.083	0.58	1.46	0.083	0.42	1.00	0.464	0.31	1.52	0.063
Residuals	240	0.29			0.40			0.42			0.21		
Transformation		none			none			none			none		

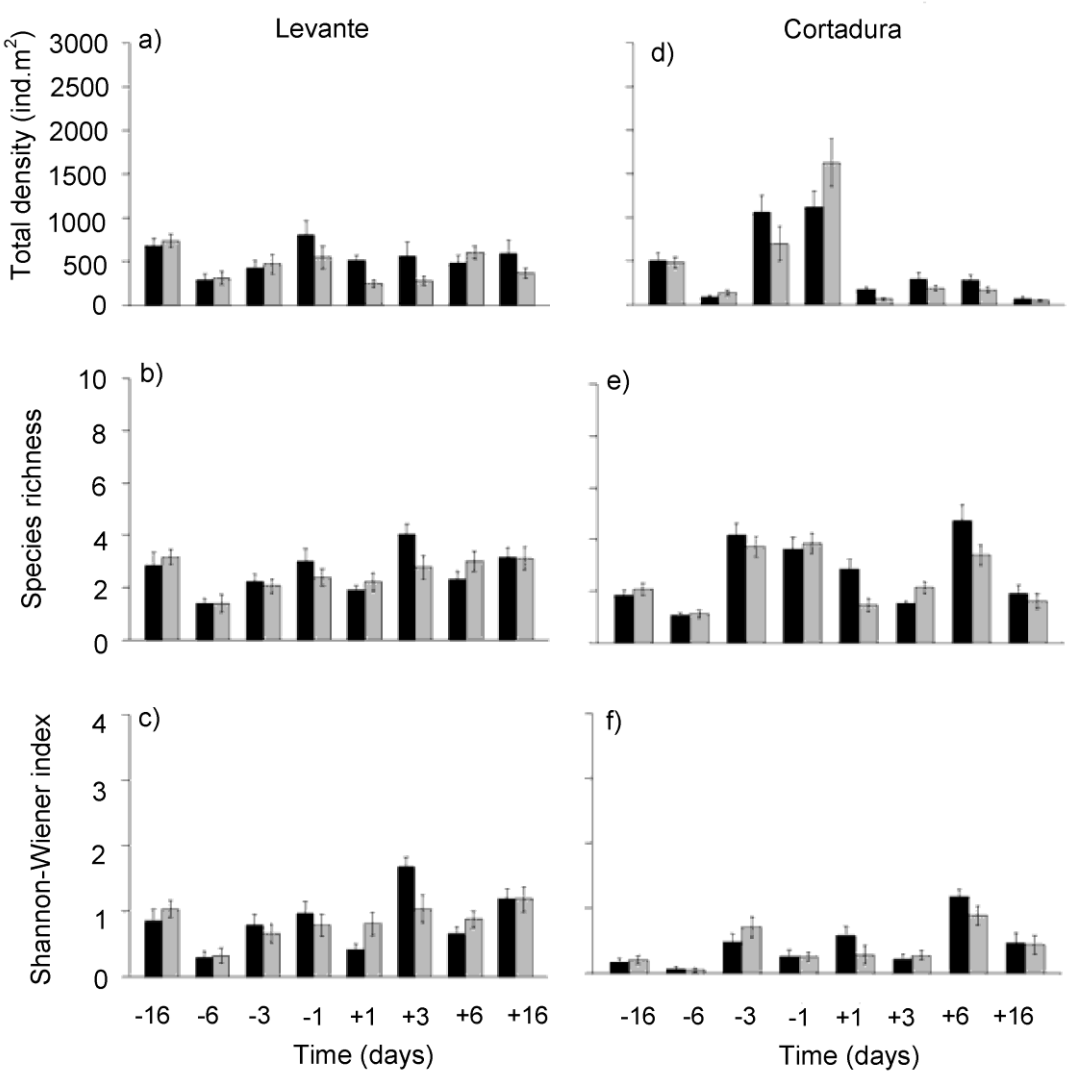

Figure 5. Spatial-temporal changes in total density (a, d), species richness (b, e) and diversity index (c, f) before (-16, -6, -3, -1 days) and after (+ 1, +3, +6, +16 days) wrack removal in the control (black column) and impacted (gray column) treatments at Levante and Cortadura beaches (SW region). Mean values ± S.E. (n=18, average of within each treatment) are represented.

Temporal variations of the overall structure of the macroinvertebrate associated with wrack debris were related to the reduction in wrack available on the upper shores. On sandy beaches from PR region, the structure of assemblages differed significantly between impacted and control plots (Table 2), although the temporal variation differed at each beach. After the wrack removal, significant differences in the community structure was detected between treatments over time (between day 1 to day 16) at Assenodi (Table 2; Fig. 6), while this pattern was detected only on day 1 at Cem (Table 2; Fig. 6).

Table 2 PERMANOVA results of the M-BACI model for supralittoral arthropods communities from the two Brazilian beaches (Assenodi and Cem) and the two Spanish beaches (Levante and Cortadura). For pairwise comparisons "≠" indicates $p<0.05$ and "=" indicates $p>0.05$. Bold values correspond to significant results

		Assenodi beach			**Cem beach**		
	df	MS	*Pseudo-F*	*P*(MC)	MS	*Pseudo-F*	*P*(MC)
Treatment=Tr	1	27656	63.60	0.007	16632	5.42	<0.001
Period=Pe	1	52578	12.86	<0.001	7603	26.00	<0.001
Plot=Pl(Tr)	4	7682.2	4.21	<0.001	3067.8	1.32	0.114
Time=Ti(Pe)	6	24992	10.80	<0.001	14827	4.84	<0.001
Tr×Pe	1	20172	4.94	**0.002**	10613	3.63	**0.006**
Tr×Ti(Pe)	6	2216.8	0.96	0.553	6543.1	2.14	**<0.001**
Pl(Tr)×Pe	4	4087.3	2.24	<0.001	2927.1	1.26	0.153
Pl(Tr)×Ti(Pe)	24	2313.6	1.27	0.012	3061.4	1.32	0.004
Residuals	240	1823.2			2317.8		
Pairwise test		Condition			Condition		
Tr×Pe		**Before:**	I = C		Tr×Ti(Pe)	**T-16:**C=I	**T-3:**C=I
						T-6:C=I	**T-1:**C=I
		After:	C > I				
						T+1:C>I	**T+6:**C=I
						T+3:C=I	**T+16:**C=I
		Levante beach			**Cortadura beach**		
	df	MS	*Pseudo-F*	*P*(MC)	MS	*Pseudo-F*	*P*(MC)
Treatment=Tr	1	1763.2	1.06	0.417	2946.6	1.14	0.360
Period=Pe	1	16727	4.77	0.005	67825	47.33	<0.001
Plot=Pl(Tr)	4	1668.7	0.79	0.733	2579.1	1.52	0.079
Time=Ti(Pe)	6	19637	7.34	<0.001	22679	7.28	<0.001
Tr×Pe	1	3124.3	0.89	0.503	1441.3	1.01	0.429
Tr×Ti(Pe)	6	3950.2	1.48	0.072	2601.1	0.83	0.698
Pl(Tr)×Pe	4	3503.3	1.65	0.034	1433.1	0.85	0.646
Pl(Tr)×Ti(Pe)	24	2673.6	1.26	0.030	3117.3	1.84	<0.001
Residuals	240	2117.7			1695.3		

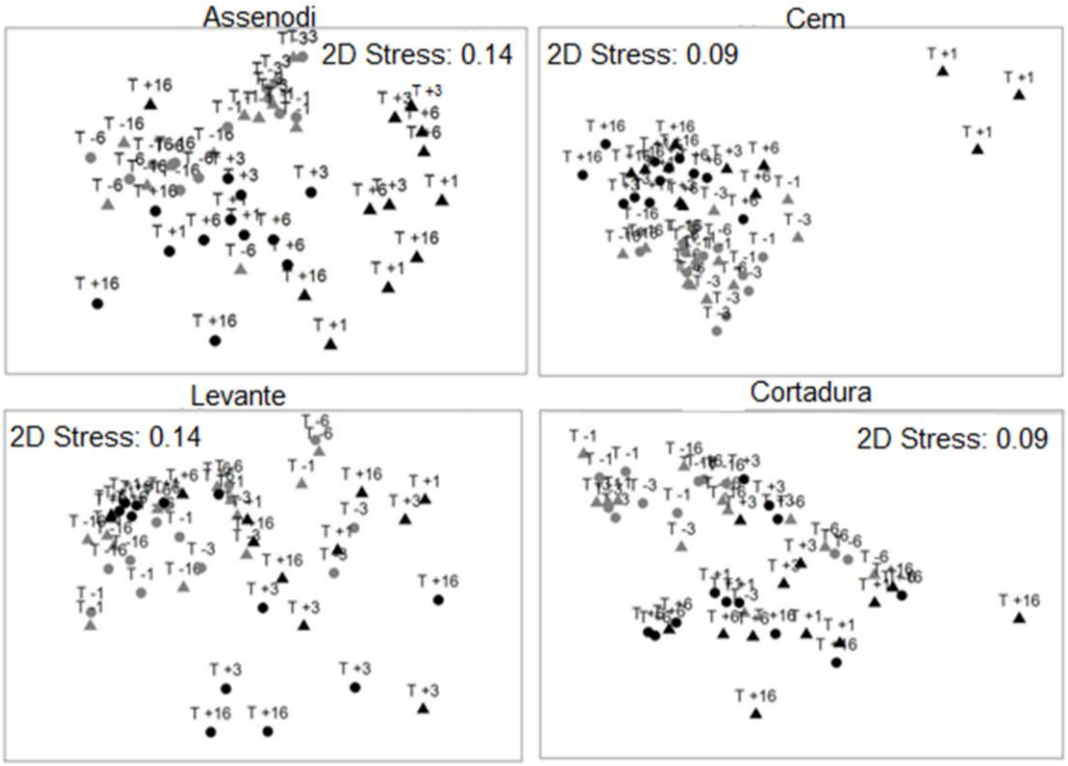

Figure 6. Non-metric multidimensional scaling (nMDS) for the comparison of supralittoral arthropod communities between control (circles) and impacted (triangles) treatments, before (-1, -3, -6, and -16 days; gray symbols) and after (+1, +3, +6, and +16 days; black symbols) the wrack removal.

Of the ten common taxa (i.e. 10% of the total samples) associated with wrack debris, changes in the density of three taxa (*Platorchestia monodi*, *Bledius bonariensis*, and Nitidulidae) at Assenodi and decline in the density of three taxa (*Platorchestia monodi*, Cleridae, and Nitidulidae) at Cem accounted for 73% and 98% of the total dissimilarity in assemblage structure between impacted and control plots, respectively (SIMPER analysis). Total density of *P. monodi* was significantly lower in the impacted than in the control plots over time at Assenodi (i.e. significant Tr×Pe; Table 3; Fig. 7a), while individuals of Nitidulidae disappeared from the impacted plots during the experiment (Fig. 7b), although significant interactions between treatments (i.e. Tr×Pe or Tr×Ti(Pe) interaction) were not detected. The mean total densities *P. monodi* and Nitidulidae was significantly lower in the impacted plots than in controls between days 1 and 3 at Cem (i.e. significant Tr×Pe; Table 3; Fig. 7e, f). Moreover, a decrease in density of Clerids was detected in the impacted plots on day +1 (Fig. 7g), although this pattern was not statistically significant (i.e. no significant Tr×Pe or Tr×Ti(Pe) interaction; Table 3). On

the other hand, the density of *B. bonariensis* registered higher values in the impacted plots than in controls after the wrack removal at Assenodi, although this pattern was not statistically significant (SNK tests p>0.05; Fig. 7a).

Table 3 ANOVA results of the M-BACI model for density of numerically dominant taxa from the two Brazilian beaches (Assenodi and Cem). Bold values correspond to significant results.

		Assenodi			**Cem**		
	df	MS	*F*	*P*	MS	*F*	*P*
(a) *P. monodi*					**(d) *P. monodi***		
Treatment = Tr	1	164.28	11.39	0.028	1355.52	9.69	0.036
Period = Pe	1	516.87	85.20	<0.001	2211.22	210.66	<0.001
Plot = Pl(Tr)	4	14.42	4.02	0.004	139.87	1.72	0.146
Time = Ti(Pe)	6	1.60	0.42	0.862	974.25	6.24	<0.001
Tr×Pe	1	178.27	29.39	**0.006**	1636.65	155.92	**<0.001**
Tr×Ti(Pe)	6	7.39	1.92	0.120	268.35	1.72	0.160
Pl(Tr)×Pe	4	6.07	1.67	0.213	10.50	0.07	0.991
Pl(Tr)×Ti(Pe)	24	3.86	1.07	0.375	156.25	1.92	0.007
Residuals	240	3.59			81.18		
Transformation			log(x+1)			(2th root)	
(b) Nitidulidae					**(e)Nitidulidae**		
Treatment = Tr	1	37.60	1.92	0.238	18.60	2.37	0.199
Period = Pe	1	43.42	5.33	0.082	60.11	42.60	0.003
Plot = Pl(Tr)	4	19.59	6.88	< 0.001	7.84	2.80	0.028
Time = Ti(Pe)	6	8.71	2.78	0.034	12.51	2.64	0.042
Tr×Pe	1	34.07	4.48	0.110	12.48	8.84	**0.041**
Tr×Ti(Pe)	6	6.68	2.13	0.086	7.34	1.60	0.206
Pl(Tr)×Pe	4	8.15	2.60	0.061	1.41	0.30	0.877
Pl(Tr)×Ti(Pe)	24	3.13	1.10	0.346	4.74	1.70	0.030
Residuals	240	2.85			2.83		
Transformation			log(x+1)			(4th root)	
(c) *B. bonariensis*					**(f) Cleridae**		
Treatment = Tr	1	48.35	1.66	0.267	44.44	5.53	0.078
Period = Pe	1	108.08	20.07	0.011	92.13	28.89	0.006
Plot = Pl(Tr)	4	29.10	9.21	<0.001	8.03	1.88	0.114
Time = Ti(Pe)	6	133.22	26.58	<0.001	32.35	3.95	0.007
Tr×Pe	1	30.10	5.59	0.077	17.16	5.38	0.081
Tr×Ti(Pe)	6	1.46	0.29	0.935	4.50	0.55	0.765
Pl(Tr)×Pe	4	5.39	1.07	0.391	3.19	0.39	0.814
Pl(Tr)×Ti(Pe)	24	5.01	1.58	0.045	8.18	1.92	0.008
Residuals	240	3.16			4.26		
Transformation			log(x+1)			log(x+1)	

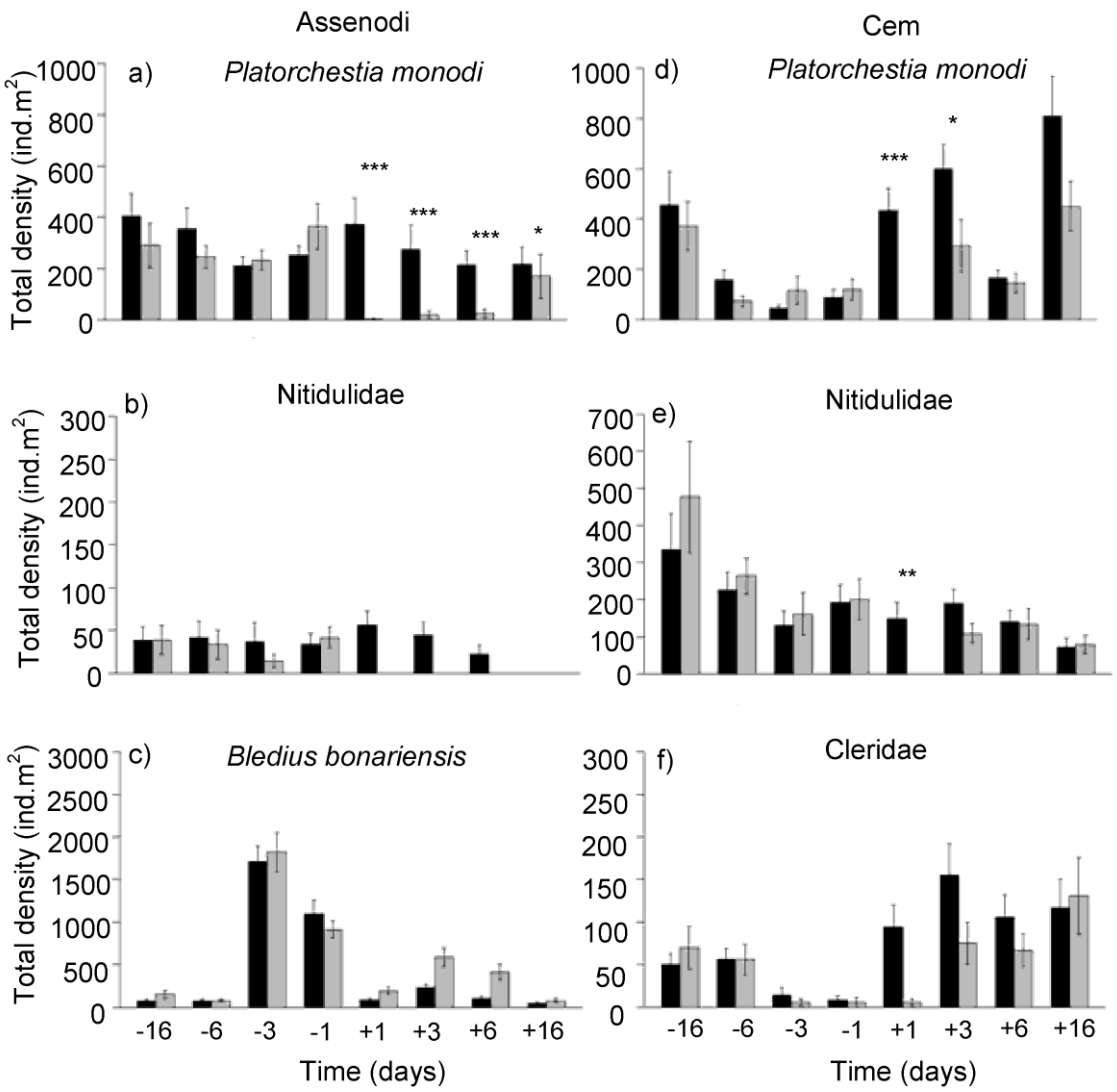

Figure 7. Spatial-temporal changes in density of numerically dominant taxa before (-16, -6, -3, -1 days) and after (+ 1, +3, +6, +16 days) wrack removal in the control (black column) and impacted (gray column) treatment for the two Brazilian beaches. a,c,e: taxa recorded at Assenodi beach; b,d,f: taxa recorded at Cem beach. Data are mean of taxa density ± S.E. (n=18, average of within each treatment). Significative differences between treatments (control and impacted) at any time was also represented (SNK tests, * p<0.05; * p<0.01; *** p<0.001).

On the other hand, macroinvertebrates associated with wrack debris were structurally similar between treatments on beaches from the SW region (i.e. no significant interaction Tr×Ti (Pe) at Levante and Cortadura; Table 2). Therefore, dissimilarity between samples collected at each treatment was not observed at any time (between days 1 to 16) after the experimental wrack removal (Fig. 6). In this region, assemblages associated with wrack debris were dominated by the amphipod *Talitrus saltator*, which comprised 85% and 95% of individuals at Levante and Cortadura beach.

Table 4 ANOVA results of the M-BACI model for density of numerically dominant taxa from the two Spanish beaches (Levante and Cortadura). Bold values correspond to significant results.

		Levante			**Cortadura**		
	df	MS	*F*	*P*	MS	*F*	*P*
(a) *T. saltator*					**(e) *T. saltator***		
Treatment = Tr	1	53.46	0.84	0.411	1125000	0.02	0.885
Period = Pe	1	683.62	2.86	0.166	2.287E+09	67.20	0.001
Plot = Pl(Tr)	4	63.58	0.90	0.464	4795434	2.39	0.052
Time = Ti(Pe)	6	835.33	12.16	<0.001	511458843	9.19	<0.001
Tr×Pe	1	65.58	0.27	0.628	23006806	0.68	0.457
Tr×Ti(Pe)	6	219.39	3.19	**0.019**	56868889	1.02	0.435
Pl(Tr)×Pe	4	238.94	3.48	0.022	34033056	0.61	0.658
Pl(Tr)×Ti(Pe)	24	68.72	0.97	0.501	55625090	2.80	<0.001
Residuals	240	70.53			19896278		
Transformation			(2th root)			none	
(b) *Brachycera* sp.					**(f) *Aleocharinae* sp. 3**		
Treatment = Tr	1	2.83	17.13	0.014	0.70	0.16	0.711
Period = Pe	1	3.44	2.70	0.176	4.52	3.69	0.127
Plot = Pl(Tr)	4	0.17	0.09	0.985	4.35	2.23	0.066
Time = Ti(Pe)	6	31.57	16.69	<0.001	53.00	19.25	<0.001
Tr×Pe	1	3.16	2.48	0.190	5.79	4.72	0.095
Tr×Ti(Pe)	6	4.16	2.20	0.078	2.58	0.94	0.488
Pl(Tr)×Pe	4	1.27	0.67	0.617	1.22	0.45	0.775
Pl(Tr)×Ti(Pe)	24	1.89	1.05	0.405	2.75	1.41	0.101
Residuals	240	1.80			1.95		
Transformation			(4th root)			(4th root)	
(c) *P. bimaculata*							
Treatment = Tr	1	0.01	0.01	0.915			
Period = Pe	1	21.89	12.71	0.023			
Plot = Pl(Tr)	4	0.69	0.61	0.657			
Time = Ti(Pe)	6	19.74	8.24	< 0.001			
Tr×Pe	1	0.51	0.30	0.615			
Tr×Ti(Pe)	6	1.85	0.77	0.600			
Pl(Tr)×Pe	4	1.72	0.72	0.600			
Pl(Tr)×Ti(Pe)	24	2.40	2.12	0.002			
Residuals	240	1.13					
Transformation			(4th root)				

The density of *T. saltator* was lower in the impacted plots than in controls on day 1 after the wrack removal at Levante beach (SNK test, $p<0.001$, Fig. 8a), while three days later no differences were detected between the two treatments (SNK test $p>0.05$) on this beach. A similar pattern was observed at Cortadura beach between days 1 and 3 after the wrack removal (Fig. 8d), although this pattern was not statistically significant (i.e. no significant Tr×Pe or Tr×Ti(Pe) interaction; Table 4).

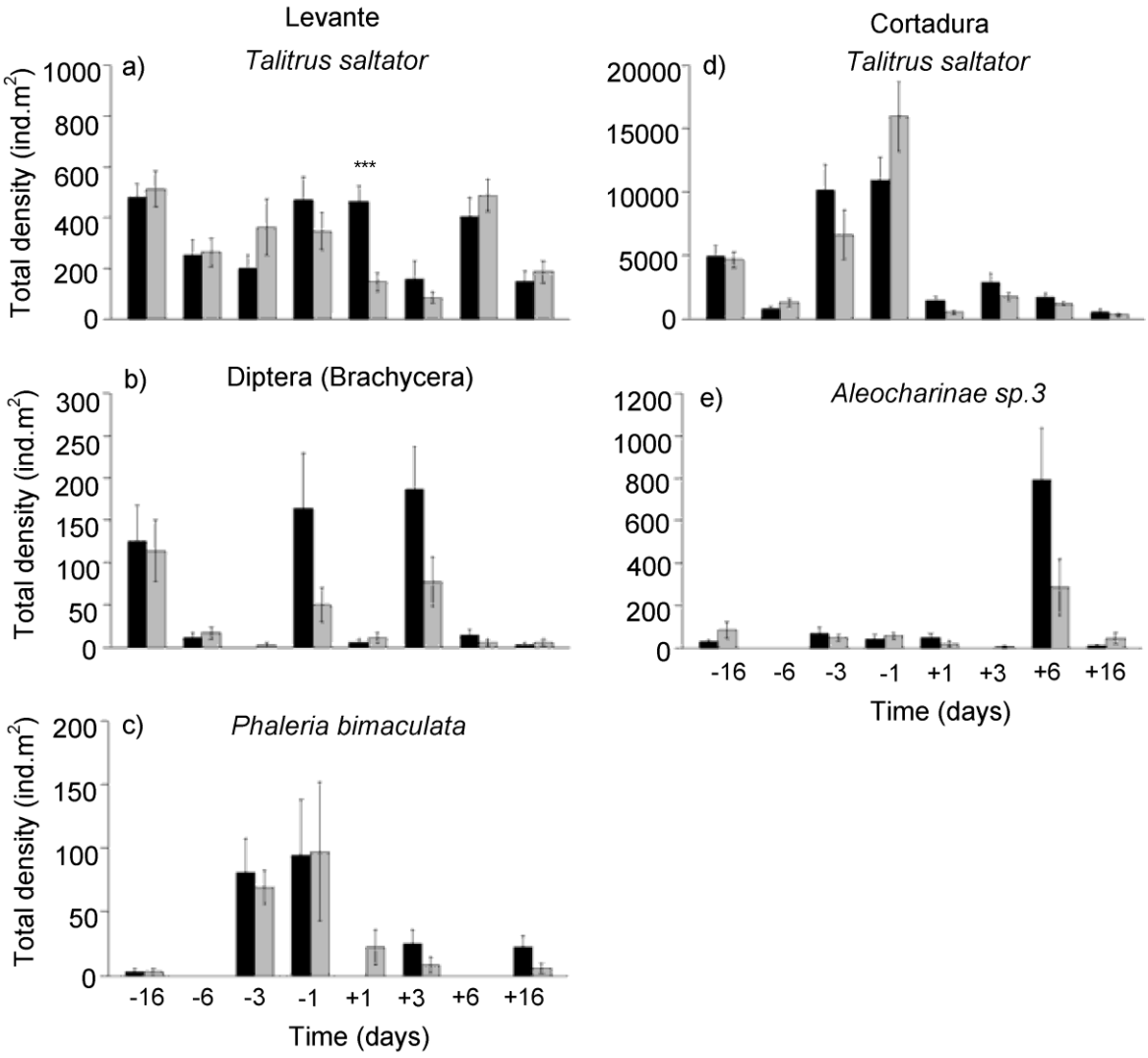

Figure 8. Spatial-temporal changes in density of numerically dominant taxa before (-16, -6, -3, -1 days) and after (+ 1, +3, +6, +16 days) wrack removal in the control (black column) and impacted (gray column) treatment for the two Spanish beaches. a-c: taxa recorded at Levante beach; d-e: taxa recorded at Cortadura beach. Data are mean of taxa density ± S.E. (n=18, average of within each treatment). Significative differences between treatments (control and impacted) at any time was also represented (SNK tests, *** $p<0.001$).

Other numerical macroinvertebrate taxa (i.e. *Phaleria bimaculata*, Aleocharinae sp3, dipterans) declined in density irrespective of whether wrack was experimentally removal or not (i.e. no significant Tr×Pe or Tr×Ti(Pe) interaction, Table 4; Fig. 8c,b,e).

DISCUSSION

Effects of wrack removal on upper-shore assemblages

Our experimental design (M-BACI) demonstrated that wrack removal, in the spatial and temporal scales used in this experiment, had an effect on wrack-associated fauna, since significant changes in community structure after the experimental removal were detected in the impacted areas with respect to the control areas. Although the removal of wrack debris along the driftlines is assumed to be a source of disturbance for strandline-associated fauna because of the loss of microhabitat refuge and/or the reduction of food source (e.g. Dugan et al., 2003; Gilburn, 2012), there are no experimental field studies showing the direct effect of the reduction of the wrack biomass on macroinvertebrate assemblages at the strandlines.

The removal of wrack resulted in changes in the structure of the communities over the short term (days to weeks), although the period of time in which the effects were measurable changed between regions. In the Paraná region, one day after the wrack removal, macroinvertebrate assemblages in the impacted areas were less abundant and diverse than in control areas, resulting in significant changes in the structure of the communities. This change was more severe at Assenodi, where community structure differed until 16 days after the wrack removal, than at Cem, where treatments were comparable at 3 days after the disturbance. On the other hand, in the SW region the removal of wrack debris did not significantly alter density, diversity, or the overall structure of the communities. We expected a stronger influence of the wrack removal on strandline communities, given the role of wrack debris as shelter and/or food source for upper-shore arthropods (e.g. Inglis, 1989; Colombini et al., 2000; Ince et al., 2007; Colombini et al., 2011a; Gonçalves and Marques, 2011; Ruiz-Delgado et al., 2015). However, our results showed that the removal of wrack debris did not appear to be severe enough to drastically change the density, or number of species or the structure of the communities probably due to the relative resilience of beach species to temporal and spatial variability of beach features (McLachlan and Brown, 2006), such as the supply of wrack biomass. In this way, a short-term impact (i.e. the wrack removal)

caused a pulse disturbance (i.e. a short-term effect on species densities) followed by a rapid recovery in the absence of new disturbances (Glasby and Underwood, 1996), and, therefore, the effects lasted for shorter time periods (days to weeks). Conversely, in managed beaches the effects of a pulse disturbance, as performed in this study, could be magnified by interaction with other sources of disturbances (trampling, recreational activities, cleaning, artificial structures, etc.) at the supralittoral zone (Fanini et al., 2005; Veloso, 2008; Colombini et al., 2011b; Bessa et al., 2014b), and therefore, the temporal extent of the effects from a short-term disturbance depicted in this work might be more protracted, as Defeo et al. (2009) reported for different beach disturbances. Future studies concerning the temporal extent of the effects of short-term (i.e. days to weeks) wrack removal on populations and/or communities associated with wrack debris on managed and unmanaged beaches are needed to support this hypothesis.

The patterns of changes detected in the communities could match the temporal changes of wrack biomass after the experimental removal from beaches of both regions (see above). In this way, strandline assemblages were structurally similar between treatments on days 3 (Cem) and 16 (Assenodi) after the wrack removal in PR region, and this pattern was observed from day 1 after the disturbance on beaches from SW region (Levante and Cortadura). From these times the amounts of stranded wrack were comparable between impacted and control areas at each beach. The availability of wrack debris has been reported as the major factor structuring supralittoral communities, mainly on beaches that receive significant inputs of wrack debris (Stenton-Dozey and Griffiths, 1983; Dugan et al., 2003; Gonçalves and Marques, 2011). Therefore, a significant and continuous input of new debris on beaches could promote a quick recovery of the communities inhabiting strandlines after the removal of strandlines.

The strandline environment is dynamic and ephemeral, and invertebrate species living there have adapted to this unique environment (Llewellyn and Shackley, 1996). For this, some behavioural strategies such as activity rhythms, orientation, zonation, burrowing, and escape responses, which are common in mobile arthropods (Brown, 1996; Scapini et al., 1997; Scapini, 2014), could be adopted by arthropods inhabiting strandlines. In our case, the removal of wrack debris and the consequent reduction of shelter source led us to hypothesise that species inhabiting strandline should exhibit behavioural strategies (e.g. rapid burrowing, escape responses, high mobility, etc.) to avoid this physical disturbance, occupying disturbed areas when wrack debris became

available on the upper shores. Accordingly, in the PR region, the short-term changes detected in the structure of the communities were attributed to the declines of the densities of some taxa (i.e. the amphipod *P. monodi* and coleopterans Cleridae, Nitidulidae and Staphylinidae) followed by recovery in the disturbed areas after the manipulation of wrack debris. However, its recovery timing varied between beaches (i.e. in 3 days at Cem and in 16 days at Assenodi), probably because of local environmental features (slight differences in position of wrack debris, in microclimatic conditions, in higher predators; interactions between and within species etc.) could be influencing the recovery of these assemblages after the wrack removal. In fact, several studies have pointed out that responses of macrofaunal assemblages to wrack deposits vary depending on sites located a few metres or kilometres apart (Colombini and Chelazzi, 2003; Dugan et al., 2003; Rodil et al., 2008). On the other hand, in the SW region of Spain, we detected no changes in the overall structure of the communities after the disturbance. A possible explanation for this response was the dominance of the amphipod *Talitrus saltator* in wrack communities (85% and 95%) and its rapid recovery (i.e. on 3 days) after the wrack removal. Therefore, it seems that the supralittoral macroinvertebrates are able recover their densities after the removal of wrack debris in both regions. Future studies on the behavioural strategies of these species are needed to understand the response patterns after a disturbance in the strandlines, especially in southern Brazil, where behavioural studies on supralittoral invertebrates are scarce.

A remarkable result was the different response pattern of the two species of talitrid amphipods (i.e. *T. saltator* and *P. monodi*) to the same source of disturbance (i.e. wrack removal) in both regions. Although both species declined in density after the removal of wrack debris, *T. saltator* recovered more quickly (3 days) than did *P. monodi* (between 6 to 16 days). Several studies on *T. saltator* have reported its behavioural strategies (i.e. orientation, zonation, burrowing abilities, high mobility, etc.) to cope with beach disturbances (Scapini et al., 1997; Fanini et al., 2005; Bessa et al., 2013; Nourisson et al., 2014) and, therefore, a quick recovery (i.e. on 3 days) could be expected after a short-term impact at the strandlines. In our case, this species could reduce the negative effects of wrack removal by burrowing deeply into the surrounding sand and by a quick displacement to closer undisturbed zones surrounding the plots (Llewellyn and Shackley, 1996). On the other hand, the more protracted recovery of *P. monodi* suggests different behavioural strategies to mitigate this disturbance. For instance, the inability to burrow, previously reported for this species (Stock, 1996;

Serejo, 2004) and its reduced mobility (personal observation) failed to reduce the likelihood of its being removed. Moreover, an active migration and concentration of organisms in undisturbed areas (e.g. dunes or vegetated backshore) was possible during the experimental removal. However, though the different movement ability of the two species might explain the different timing of recovery in the absence of new disturbances. Nevertheless, studies on behavioural adaptations of the amphipod *P. monodi* are needed to test this hypothesis. The scarce information concerning the behaviour of Talitridae species on the Atlantic coast of South America (e.g. Brazilian coast) make it difficult to explain the response patterns of this taxonomic group. The different response patterns of the wrack-associated fauna to a same source of disturbance (i.e. wrack removal) in both geographical regions (SW and PR regions) suggest the need of comparative research effort, to increase our knowledge about the behavioural strategies of supralittoral arthropods and ecosystem resilience (Scapini, 2014).

Implications for beach management

Our results suggested that localized and short-term removal of stranded organic debris on undisturbed upper shores may result in detectable changes in the density of some species and therefore in community structure, but these communities appear to be recover rapidly. Therefore, in non-urban beaches, a localized manual removal of organic debris will certainly not result in drastic reductions in density or diversity of the communities inhabiting strandlines. However, the timing of recovery will probably depend on the amount and temporal dynamics of wrack biomass at the strandlines and the behavioural adaptations of species associated with wrack debris. Our results suggest that these could be important factors to analyse the effects of disturbances on strandline environments.

Since strandlines support rich supralittoral fauna of crustaceans and insects, which cannot be found in any other environment (Colombini and Chelazzi, 2003) and play key roles in the ecosystem functioning (e.g. Jędrzejczak, 2002a; Dugan et al., 2003; Mews et al., 2006; Lastra et al., 2008; Gonçalves and Marques, 2011), minimizing the human impact on the wrack-associated fauna is crucial to maintain the functional integrity of beach ecosystems (Defeo et al., 2009). A possible management strategy could be to adapt the methods of cleaning (mechanical or manual) to the type of beach under question (urban or non-urban) (Micallef and Williams, 2002), and, therefore,

manual removal of organic debris and unwanted beach litter in natural beaches could help maintain the biodiversity associated with strandlines, as our results suggest. Moreover, this type of cleaning minimally disturbs the strandline habitat and could encourage the dune formation through the retention of sand supply (Dugan and Hubbard, 2010). Because beach visitors tend to aggregate in relative small areas of the beaches (de Ruyck et al., 1998; Schlacher and Thompson, 2012), wrack debris could be locally removed from small areas along the shore interspaced with uncleaned areas. This could be a mitigation strategy of the negative effect of wrack removal on macroinvertebrate assemblages, as our results suggest. However, this strategy was tested at a small spatial scale (i.e. 100 m along-shore), and therefore field experiments at larger spatial scales are needed to test the effect of localized removal of wrack debris on supralittoral macroinvertebrates.

In summary, this study provides fundamental quantitative information on the short-term effects of wrack removal on strandline-associated macroinvertebrates on sandy beaches. The removal of stranded organic debris resulted in detectable changes in the density of some species and therefore in community structure, but these rapidly recovered, although the timing of recovery differed in communities inhabiting the upper shores of each region. The dynamics of the wrack supply and the species-specific adaptations of invertebrates inhabiting the strandlines might determine the response of the assemblages to the same source of disturbance (i.e. wrack removal) on beaches located on both sides of the Atlantic Ocean. However, future studies on the behavioural strategies (e.g. mobility, burrowing) of species and the interaction with environmental factors (e.g. composition and features of wrack debris) are needed in order to understand the mechanisms involved in the different response patterns of supralittoral macroinvertebrates subjected to wrack removal.

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WRACK REMOVAL AS SHORT-TERM DISTURBANCE FOR *TALITRUS SALTATOR* DENSITY ON THE SANDY UPPER BEACHES: AN EXPERIMENTAL APPROACH

Wrack removal as short-term disturbance for *Talitrus saltator* density on sandy upper beaches: an experimental approach

ABSTRACT

A distinctive feature of exposed sandy beaches is the stranded wrack which provides a direct source of food and/or shelter for supralittoral macroinvertebrates. Wrack debris is commonly removed from sandy beaches worldwide, but experimental studies concerning its effect on strandline macrofaunal species are scarce. Since *Talitrus saltator* is considered an effective bioindicator on sandy beaches, it was used to assess the effect of the removal of wrack as a short-term disturbance. For this, a field experiment, following an M-BACI design, was conducted on two sandy beaches on the European Atlantic coast (SW Spain). Our results showed for the first time that the removal of wrack biomass did diminish the density of *T. saltator* associated with wrack debris, although the recovery to pre-disturbance levels was fast. Juveniles appear to be more sensitive to this disturbance than adults, although this pattern apparently depends on the density of *T. saltator* that, in turn, may depend on the beach type and the wrack composition. Our experiment demonstrated that although a decline in density of *T. saltator* was detected after the removal of wrack, this talitrid amphipod was able to cope with a short-term disturbance in wrack supply (i.e. pulse disturbance). This study highlights the strong adaptability of this amphipod species to quick changes in the strandline environment.

Keywords: disturbance; wrack; amphipod; age classes; beaches; Southwest of Spain.

INTRODUCTION

Ocean sandy beaches are dynamic environments that make up two-thirds of the open coastlines (McLachlan and Brown, 2006). Burgeoning population growth in coastal areas, coupled with more leisure time and improved mobility, have escalated the intensity and spatial ambit of beach recreation over recent decades (Brown and McLachlan, 2002; Defeo et al., 2009). This increasing use of sandy beaches as recreational places has encouraged the removal of wrack debris in order to improve the aesthetics, amenity, utility, and health of sandy beaches (Fairweather and Henry, 2003). However, this activity could influence on the ecosystem functioning because exposed sandy beaches are characterized by a low in situ primary production, and thus beach food webs depend largely upon allochthonous inputs from the sea and coastal areas (Griffiths et al., 1983; Colombini and Chelazzi, 2003; Dugan et al., 2003). These inputs support beach consumers, mainly supralittoral crustaceans such as talitrid amphipods and oniscid isopods, which occupy a key position in food chains as trophic intermediates between algal wrack and higher trophic levels (Griffiths et al., 1983; Brown and McLachlan, 2002; Dugan et al., 2003; McLachlan and Brown, 2006).

The sandhopper *Talitrus saltator* (Montagu, 1808) is a common and widespread (Mediterranean, Baltic and Eastern Atlantic coasts) inhabitant of exposed sandy beaches (Weslawski et al., 2000a; Colombini et al., 2002; Gonçalves et al., 2009; Rodil et al., 2006). In general, talitrid amphipods live buried between the driftline and the base of the foredunes during the day, emerging at night to feed and move across the shoreline (Scapini, 2006). The availability of wrack on sandy beaches influences the distribution of talitrid amphipods (Stenton-Dozey and Griffiths, 1983; Gonçalves and Marques, 2011), particularly on the upper shores, where their abundance is higher under wrack debris than in the nearby bare sand (Jaramillo et al., 2006; MacMillan and Quijon, 2012; Ruiz-Delgado et al., 2015). Moreover, on sandy shores with high amounts of wrack, talitrid amphipods tend to concentrate at the supratidal, and even become restricted to the driftlines, using stranded wrack as food and/or shelter (Gonçalves and Marques, 2011; Bessa et al., 2014a). To inhabit a highly dynamic ecosystem such as sandy beaches, talitrid amphipods have developed behavioural adaptations, including mobility, burrowing abilities, rhythmicity in their behaviour and orientation plasticity (Brown, 1996; Scapini, 1997; Nardi et al., 2003; Scapini, 2006; Rossano et al., 2009), which change with the development stage of individuals (Williams, 1983; Scapini et al., 1992;

Scapini, 1997, 2006). The behavioural plasticity gives them high tolerance towards diverse stressful conditions (e.g. extreme temperatures and humidities, chemical pollution, change in the sediment size, decreased food availability), although this tolerance is not unlimited. In this context, several studies have reported the sensitivity of sandhoppers to physical disturbances in sandy beaches such as dune rehabilitation, nourishment processes, beach cleaning, artificial infrastructures, and activities linked to tourism, which alter the population density and, in some cases, also the behavioural responses of these macroinvertebrates (Weslawski et al., 2000b; Nardi et al., 2003; Fanini et al., 2007, Veloso et al., 2008; Fanini et al., 2009; Scapini and Ottaviano, 2010; Bessa et al., 2013).

Most sandy beach studies used "compare and contrast" design in which *existing* assemblages are sampled in the putatively impacted area and in controls, whereas experiments are few in these habitats (e.g. Schlacher and Morrison, 2008; Lucrezi et al. 2009; Schlacher and Lucrezi, 2010; Walker and Schlacher, 2011). In this design is difficult to recognise the cause/s of a perturbation and, therefore, the cause-effect relationships. Contrary, manipulative experiments could be a good way to evaluate the direct effect of environmental disturbances (Glasby and Underwood, 1996). Nevertheless, experimental studies are difficult to perform in sandy beaches, because of these systems are spatially and temporally heterogeneous habitats, in which populations undergo fluctuations from one time to another that are not comparable from place to place (McLachlan and Brown, 2006; Schlacher et al., 2008). As a result, there is considerable interaction between space and time in the data from any sampling design. Therefore, any experimental design in sandy beaches, required to robust methods to measure any potential changes in the mean numbers of the target species over space and time (*sensu* Underwood, 1994). In this way, M-BACI (multiple before-and-after control-impact) design includes multiple control and impact locations which are sampled repeatedly before and after the disturbance (Underwood, 1994; Downes et al., 2004). This design allows an appropriate spatial and temporal replication (i.e. multiple locations and several times of samplings) to analyse the response of natural communities and/or populations to environmental disturbances in sandy beaches. To our knowledge, M-BACI methodology has not been previously used to evaluate the effect of disturbances on sandy beaches.

The removal of wrack has significant ecological consequences for beach and nearshore ecosystems (e.g. Kirkman and Kendrick, 1997; Lavery et al., 1999; Dugan et

al., 2003; Fairweather and Henry, 2003; Piriz et al., 2003; Gilburn, 2012). The reduction of wrack biomass could mean a loss of habitat and food sources with a consequent reduction in the abundance and diversity of supralittoral macrofauna such as talitrid amphipods, oniscoid isopods, and insects (Colombini et al., 2000; Dugan et al. 2003; Fairweather and Henry, 2003; Gilburn, 2012). Moreover, this disturbance could have a cascading effect of the coastal food webs (Spiller et al., 2010). The removal of driftlines, as well as their associated fauna, could result in a loss of recycled nutrients and detrital material, which form the basis for primary production and food chains of nearshore waters (Kirkman and Kendrick, 1997; Dugan et al., 2011; Barreiro et al., 2013). Therefore, it is important to understand the ecological effects of wrack on sandy beaches prior to its wholesale removal (Fairweather and Henry, 2003). However, there are no field experimental studies available to evaluate the effect of wrack removal on macroinvertebrates inhabiting sandy beaches such as supralittoral arthropods.

In this study we carried out a short-term field experiment, following M-BACI design, to quantify, for the first time, the effect of a source of disturbance, i.e. wrack removal, using the bioindicator *T. saltator* on two sandy beaches. It was hypothesised that the reduction of stranded wrack biomass by experimental removal would lower the total density of the amphipod *T. saltator* associated with stranded wrack at the supralittoral zone, where wrack debris are used as food and/or shelter source. We also hypothesised that the remove of strandlines could have a different effect on the density of adults and juveniles in relation to their different size and behavioural responses.

MATERIALS AND METHODS

Study site

The field experiment was conducted on Levante and Cortadura beaches, located on the Atlantic coast of Cadiz (SW Spain) (Fig.1). These beaches have natural and ungroomed backshores and both of them receive allochthonous inputs (i.e. wrack) from the sea. The Gulf of Cadiz is a semidiurnal mesotidal environment with a tidal range between 3.2 and 1.1 m (Benavente et al., 2002). Wave height is usually lower than 1 m although storms cause heights of up to 3 m, classifying the area as a low-energy coast (Benavente et al., 2000). Levante (36°33’37’’N; 6°13’27’’W), is a dune-backed, dissipative beach with fine-sized sand (mean grain size = 0.18 mm) and gentle slope (3.55%). The intertidal width of the beach from the edge of the dunes to the low swash is ~ 100 m.

During this study, Levante beach received inputs of the seagrasses *Cymodocea nodosa* (39%) and *Zostera noltii* (61%) from seagrass beds located around Cadiz Bay (Pérez-Lloréns et al., 2013). Cortadura (36º28'58''N; 6º15'77''W), is an intermediate beach, backed by foredunes and low vegetated dune ridges, with fine-sized sand (mean grain size = 0.23 mm) and gentle slope (3.82%). The intertidal width of the beach is ~ 85 m. Cortadura was subsidized by brown macroalgae (66%) such as *Dictyopteris membranacea* and *Cladostephus spongiosus*, several species of red macroalgae (29%) such as *Halopithys incurva* and *Chondria dasyphylla* and green macroalgae (5%) such as *Codium decorticatum* and *Codium fragile* from nearby rocky shores and subtidal habitats (Pérez-Lloréns et al., 2013).

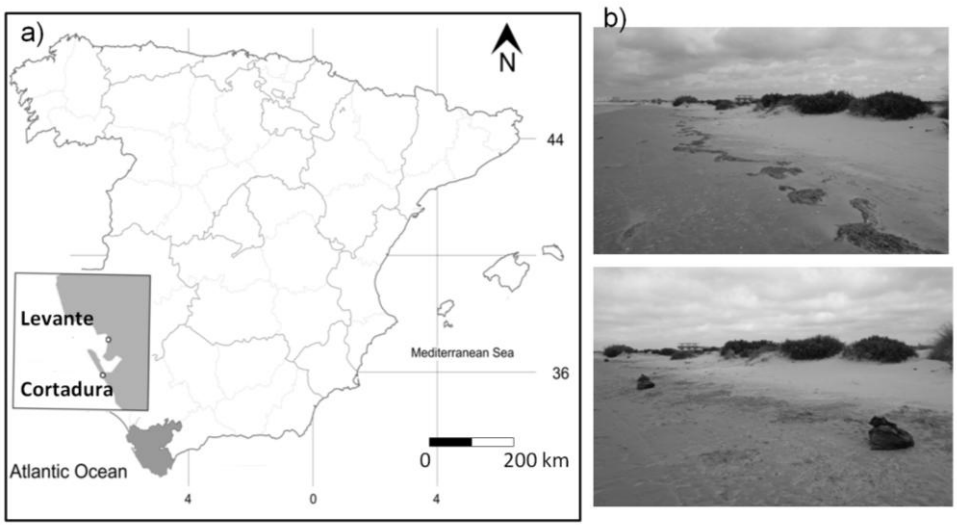

Figure 1. Sites of field experiment. a) Location of the 2 exposed sandy beaches (Levante and Cortadura) on the south-western coast of Spain; b) Levante before and after all natural wrack debris were removed from the beach surface.

Experimental design and data collection

A field experiment, following the M-BACI design, was performed between 2 October and 12 November 2012 at Levante and Cortadura beaches. The M-BACI sampling strategy is considered appropriate for analysing planned perturbations (Keough and Mapstone, 1997; Underwood, 2000; Downes et al., 2004). This design includes multiple control and impacted locations which are compared in multiple sampling dates within before (baseline samples) and after start-up the impacting activity. The underlying assumption in this approach is that the impacted locations would have behaved approximately the same as the control locations in the absence of the disturbance

(Underwood 1994; Keough and Mapstone 1997; Downes et al., 2004). Therefore, a disturbance could inferred if changes at the impacted locations differed from those at the control locations, due to the impacted locations depart from 'normal' behaviour (Downes et al., 2004).

For this sampling design, an experimental area 115 m long was delimited and was divided into six plots, three control (C) and three impacted (I), each of 15 m wide (alongshore), extending from the base of the dune to the high tide level at each beach. The plots were positioned 5 m apart, using and interspersed design (*sensu* Hulbert, 1984). Biological responses were compared between impacted and control plots on eight sampling days: before (day -16, -6, -3 and -1) and after (day +1, +3, +6 and +16) the 10-days experimental removal (Fig. 2). At each impacted plot, we raked and eliminated all wrack debris that had accumulated into the plots (Fig. 1) and those present at the 5m intervals bordering impacted plots. Moreover, wrack debris deposited at the intertidal zone was also eliminated. This experimental removal was performed during 10 consecutive days to ensure a reduction of wrack biomass and, therefore, an expected reduction of the density of amphipods at the strandlines. During the before and the after periods (Fig. 2) the tidal coefficients were similar (ranging between 0.80-1.08 and 0.80-1.00, respectively) to avoid that tidal regime can mask the effect of wrack removal on the density of *T. saltator* at the supratidal.

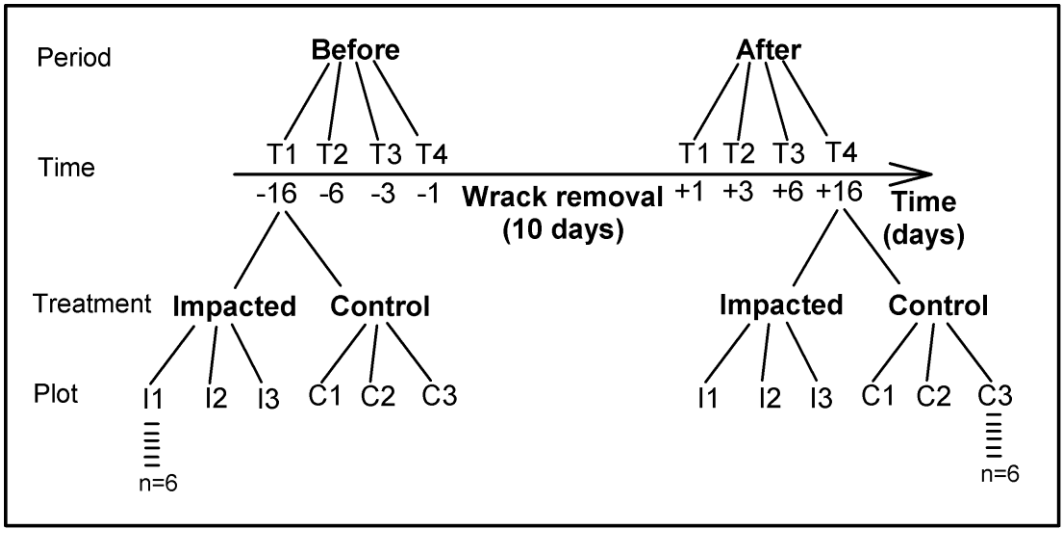

Figure 2.M-BACI design used in the field experiment and the data analysis. T =Time (days); I (impacted) and C (control) plots; n=numbers of samples in each plot and at each day.

On each sampling date, wrack coverage was measured from photographs taken within six 1x1 m quadrats placed randomly in each treatment plot (i.e. 144 photographs per treatment). Amphipods associated with wrack debris and those that had burrowed underneath the wrack patches were collected. For this, algal wrack at the surface and 20 cm of sediment were taken with a 15-cm diameter PVC core. At its free end, a plastic bag was used to prevent talitrids from escaping. Six fauna samples were collected per plot at randomly chosen seaweed patches. Each sample was taken from a 1x1 m quadrat within each treatment plot (i.e. 144 samples per treatment). Samples were transferred into 70% ethanol. All samplings were conducted during the morning to ensure the capture of talitrids of both ages (adults and juveniles) at the upper-shores, since amphipods tend to remain either hidden under wrack debris and/or burrow in the sand underneath wrack patches to avoid drying from sun (e.g. Scapini, 2006).

In the laboratory, the samples were washed and sieved through a 0.5 mm mesh. All wrack debris was dried to a constant weight at 60ºC (g dw). The coverage was estimated as the percentage of plot surface (1x1 m quadrat) covered by wrack patches using ImageJ (v. 1.45) (Abràmoff et al., 2004). For an estimate of the stranded wrack biomass (g dw/m^2) in each plot, the percentage of coverage was applied to values of biomass (g dw) per core of each sampling date. The amphipods were counted under binocular microscopes and then were sorted according to the age (i.e. adults and juveniles), by counting the number of articles of the second antennal flagellum (juveniles $\leq$ 14) (Fallaci et al., 2003). The total density and density of adults and juveniles of *T.saltator* in wrack patches were calculated and expressed as the number of individuals per m^2 of the surface covered by wrack debris.

Data analysis

Wrack biomass, total density and density of adults and juveniles of strandline *T. saltator* were analysed by ANOVAs, following the procedures described by Underwood (2000) and Downes et al. (2004) for the M-BACI sampling strategy. A 4-way analysis of variance was used, and included the following factors (Fig.2): treatment (Tr, 2 levels: control and impact, fixed and orthogonal), plot (Pl, 3 levels, random and nested in each treatment), period (Pe, 2 levels: before and after impact, fixed and orthogonal), and sampling time (Ti, 4 levels, fixed and nested within each period). The effect of wrack removal on *T. saltator* densities was identifiable as interactions between treatment and period (i.e. Tr×Pe) or as differences among treatments at any particular time after the

experimental wrack removal (i.e. Tr×Ti(Pe)) on each studied beach. These interactions are the only terms of interest in order to quantify the effect of this disturbance.

Homogeneity of variances was analysed by Cochran tests and normality was examined through visual inspection of residual and probability plots. Data were squared-root or log (x+1) transformed if variances were significantly different at p=0.05. For non-homogeneous variances, ANOVA was, nevertheless, used after setting p=0.01, to reduce the chance of Type I error (Underwood, 1997). Significative effects and interactions were examined using the Student-Newman-Keuls (SNK) multiple-comparison test (p=0.05). All statistical analyses were performed using the GAD package (Sandrini-Neto and Camargo, 2013) in R 2.15.2 (R Development Core Team, 2012).

RESULTS

Wrack biomass

The wrack supply was different on both beaches during the study. Thus, the standing crop was 34.96 g dw/m^2 on Levante and 53.88 g dw/m^2 on Cortadura. During the field experiment, wrack biomass showed different temporal patterns in the control and impacted plots on both beaches (Fig. 3). At Levante beach, the wrack biomass varied between plots within each treatment from one time to another (significantly Pl(Tr)×Ti(Pe) interaction; Table 1). After manipulation, the mean of wrack biomass was significantly lower in the impacted than in the control plots on day +1 and +3 (SNK test $p<0.001$; Fig. 3), while on day +6 the wrack biomass rose again to more values more similar to those of the control plots (SNK test $p>0.05$). The same pattern was observed on day +16 (SNK test $p>0.05$). At Cortadura beach, the average of wrack biomass differed among treatments from one time to another after wrack removal (significantly Tr×Ti(Pe) interaction; Table 1). One day after the impact, the mean of wrack biomass was significantly lower in the impacted than in the control plots (SNK test $p<0.001$; Fig. 3), while three days later, no differences were detected between the two treatments (SNK test $p>0.05$). The average wrack biomass remained equal between treatments on day +6 and +16 (SNK test $p>0.05$; Fig. 3).

Table 1 Summary of the ANOVA results for wrack biomass from the two studied beaches (Levante and Cortadura). Treatment (2 levels: control and impact), Period (2 levels: before and after impact), Sampling time (4 levels, nested within each period) are fixed factors, and Plot (3 levels, nested in each treatment) is random factor. Degrees of freedom (df) and MS=mean square are shown. ***p<0.001; **p<0.01; and *p< 0.05.

		Levante		Cortadura	
Source	df	MS	F	MS	F
Wrack biomass					
Treatment=Tr	1	17.69	26.65**	4.75	18.06*
Period=Pe	1	0.10	0.47	48.06	269.48***
Plot= Pl (Tr)	4	0.66	3.90**	0.26	1.08
Time= Ti (Pe)	6	6.85	19.38***	7.24	25.16***
Tr×Pe	1	11.77	57.06**	0.35	1.98
Tr×Ti (Pe)	6	3.67	10.37***	1.22	4.23**
Pl (Tr)×Pe	4	0.21	0.58	0.18	0.62
Pl (Tr)×Ti (Pe)	24	0.35	2.08**	0.29	1.18
Residuals	240	0.17		0.24	
Transformation		(4th root)		(4th root)	

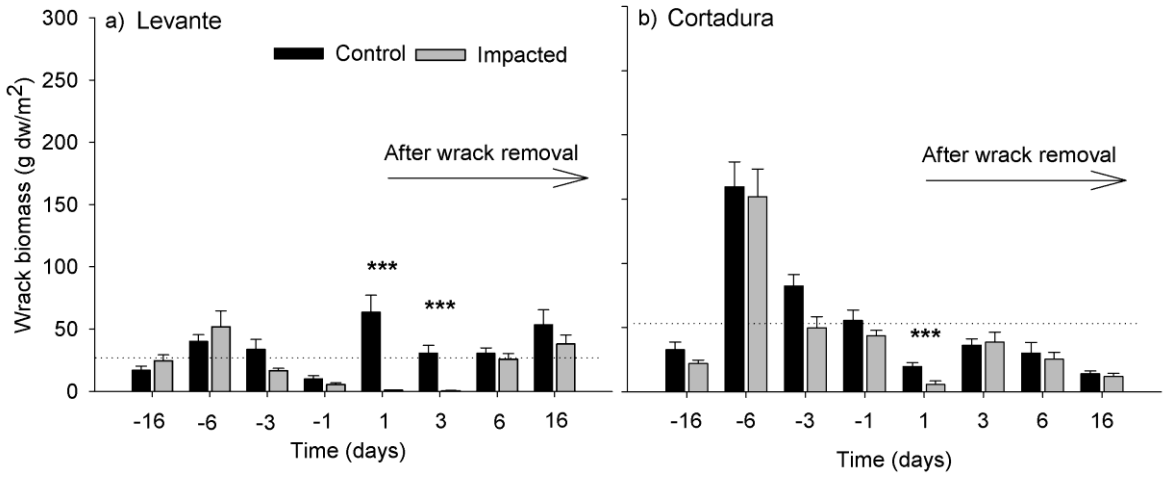

Figure 3. Temporal changes in wrack biomass (g dw/m^2) before (-16,-6,-3,-1 days) and after (1, 3, 6, 16 days) wrack removal in the control and impacted plots. Data are mean of wrack biomass ± S.E. (n=18, average of treatment plots). Significant differences between treatments (control and impacted) after the impact at any time was also represented (SNK tests, *p<0.05, **p<0.01, ***p<0.001). Dotted lines represent the average wrack biomass.

Changes in densities of strandline Talitrus saltator

An effect of wrack removal is inferred if the density of *T. saltator* at impacted locations is lower than those at the control locations at any time during the after period. Immediately after the disturbance, the mean total density was significantly lower (-69%) in the impacted (167 ± 43 ind.m^{-2}) than control plots (Table 2, Tr×Ti(Pe) interaction; SNK test $p<0.001$; Fig.4a) at Levante beach. Total density of amphipods was comparable between both treatments three days later the disturbance (SNK test $p>0.05$). The mean total density remained equal between treatments on day +6 and +16 (SNK test $p>0.05$; Fig. 4a). The density of juveniles showed a similar pattern. Its density was significantly lower (-77%) in the impacted (104 ± 28 ind.m^{-2}) than control plots (451 ± 65 ind.m^{-2}) on day +1 (Table 2, Tr×Ti(Pe) interaction; SNK test $p<0.001$; Fig. 4b), while on day +3 their density rose again to values more similar to those of the control plots (SNK test $p>0.05$). This pattern was also observed on days +6 and +16 after the wrack removal (SNK test $p>0.05$). On the other hand, the density of adults not differed significantly between treatments (control: 91 ± 18 ind.m^{-2}, impacted: 63 ± 17 ind.m^{-2}) one day after the wrack removal (i.e. no significant Tr×Ti(Pe) interaction; Table 2; Fig. 4c), and this pattern was detected over the time after the disturbance (Fig 4c).

At Cortadura beach, the total density of *T. saltator* was depressed by 63% in impacted plots (control: 1650 ± 351 ind.m^{-2}; impacted: 606 ±177 ind.m^{-2}) one day after the disturbance (Fig 5a). A similar pattern was detected for juveniles (Fig 5b), which mean density was depressed by 47% in impacted plots on day +1 (control: 1082 ± 248 ind.m^{-2}, impacted: 574 ±178 ind.m^{-2}). However, significant Treatment x Period (nested time) interaction was detected because of the power to detect this interaction was reduced by variations in change patterns over time among plots nested within treatments (i.e. significantly Pl(Tr)×Ti(Pe) interaction, Table 2). Because of a small-scale spatial variability in density, not all plots within the treatments responded equally to the treatments over time. This variability can mask a clear response pattern after the disturbance. On the other hand, the density of adults (Fig. 5c) did not show significant differences between treatments (control: 438 ± 205 ind.m^{-2}, impacted: 131 ± 30 ind.m^{-2}) after the wrack removal at any time (i.e. no significant Tr×Ti(Pe) interaction; Table 2), nor did variations in density among plots nested within treatments was detected (i.e. no significant Pl(Tr) ×Ti(Pe) interaction; Table 2).

Table 2 Summary of the ANOVA results for total density, density of juveniles and adults of *Talitrus saltator* from the two studied beaches (Levante and Cortadura). Treatment (2 levels: control and impact), Period (2 levels: before and after impact), Sampling time (4 levels, nested within each period) are fixed factors, and Plot (3 levels, nested in each treatment) is random factor. Degrees of freedom (df) and MS=mean square are shown. ***p<0.001; **p<0.01; and *p< 0.05.

			Levante	**Cortadura**	
Source	df	MS	F	MS	F
Total					
Treatment=Tr	1	0.57	1.01	449.99	0.02
Period=Pe	1	6.72	3.04	914853.55	67.2**
Plot= Pl (Tr)	4	0.56	0.78	18998.17	2.38
Time= Ti (Pe)	6	9.14	12.18***	204583.53	9.19***
Tr×Pe	1	0.49	0.22	9202.72	0.67
Tr×Ti (Pe)	6	2.27	3.03*	22747.55	1.02
Pl (Tr) ×Pe	4	2.20	2.94*	13613.22	0.61
Pl (Tr)×Ti (Pe)	24	0.75	1.04	22250.03	2.79***
Residuals	240	0.71		7958.511	
Transformation			(log x+1)	a	
Juveniles					
Treatment=Tr	1	0.17	0.79	238.34	0.01
Period=Pe	1	5.18	7.31	763436.05	67.46**
Plot= Pl (Tr)	4	0.21	0.65	15627.23	2.31
Time= Ti (Pe)	6	5.59	13.49***	177717.71	8.99***
Tr×Pe	1	0.03	0.04	11249.99	0.99
Tr×Ti (Pe)	6	1.27	3.08*	17054.99	0.86
Pl (Tr)×Pe	4	0.70	1.70	11316.18	0.57
Pl (Tr)×Ti (Pe)	24	0.41	1.24	19746.9	2.92***
Residuals	240	0.33		6746.41	
Transformation			4th root	a	
Adults					
Treatment=Tr	1	0.19	0.36	6.05	4.67
Period=Pe	1	0.00	0.00	59.45	98.81***
Plot= Pl (Tr)	4	0.54	1.76	1.29	1.54
Time= Ti (Pe)	6	1.03	4.51**	22.94	25.68**
Tr×Pe	1	0.40	0.46	0.88	1.47
Tr×Ti (Pe)	6	0.20	0.90	2.06	2.31
Pl (Tr)×Pe	4	0.86	3.75*	0.6	0.67
Pl (Tr)×Ti (Pe)	24	0.23	0.74	0.89	1.06
Residuals	240	0.30		0.83	
Transformation			(log x+1)	(log x+1)	

a. Cochran test no significant after transformation

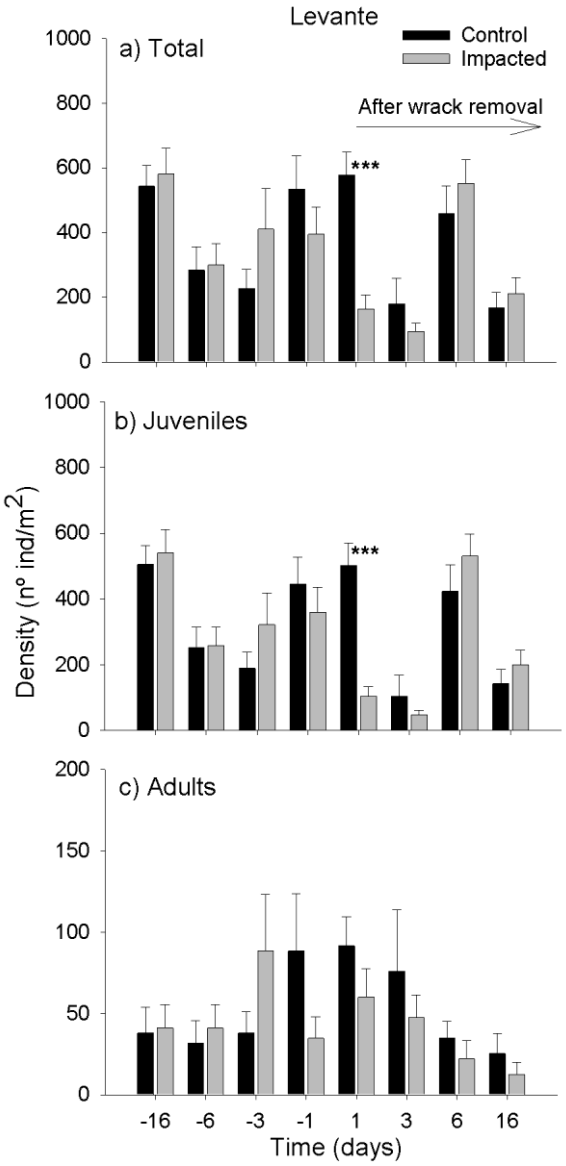

Figure 4. Temporal changes in total density (a), density of juveniles (b), and adults (c) of *T. saltator* associated with wrack deposits before (-16,-6,-3, -1 days) and after (1, 3, 6, 16 days) wrack removal in the control and impacted plots at Levante. Data are mean of density (nº ind./m^2) ±S.E. (n=18, average of treatment plots). Significant differences between treatments (control and impacted) after the impact at any time was also represented (SNK tests, *p<0.05, **p<0.01, ***p<0.001).

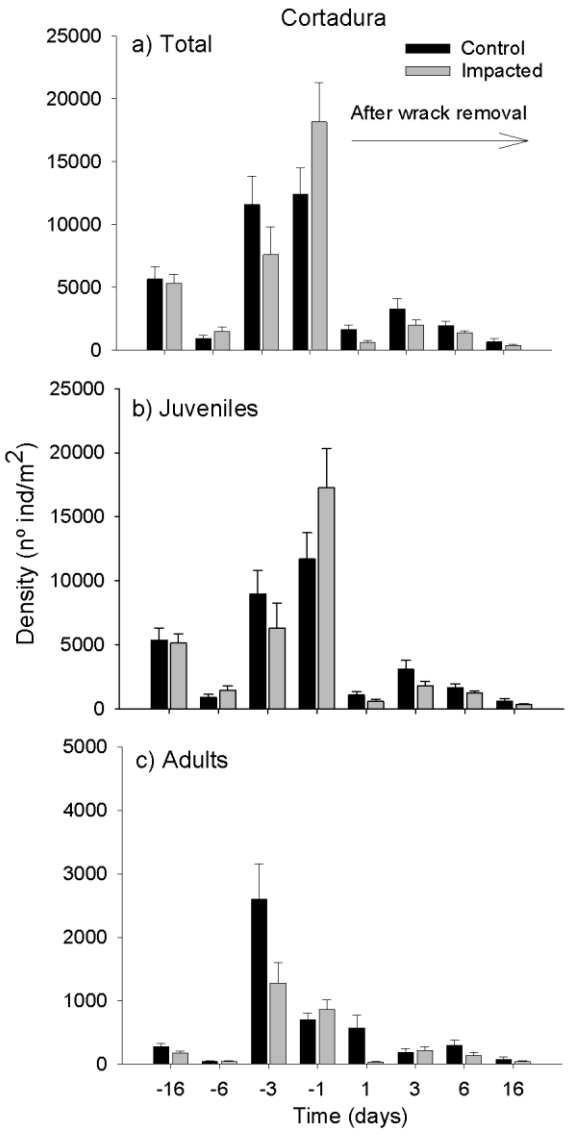

Figure 5. Temporal changes in total density (a), density of juveniles (b), and adults (c) of *T. saltator* associated with wrack deposits before (-16,-6,-3, -1 days) and after (1, 3, 6, 16 days) wrack removal in the control and impacted plots at Cortadura. Data are mean of density (nº ind./m^2) ±S.E. (n=18, average of treatment plots). Significant differences between treatments (control and impacted) after the impact at any time was also represented (SNK tests, *p<0.05, **p<0.01, ***p<0.001).

DISCUSSION

A large proportion of research on sandy beaches is based on descriptive or mensurative (i.e. contrast and compare approach) experiments rather than manipulative experiments, which are more common in other intertidal habitats (Underwood, 2000). However, manipulative experiments allow for greater confidence in our inferences about cause and effect than mensurative experiments (Gotelli and Ellison, 2004). To the best of

knowledge, this study is the first experiment which manipulated wrack biomass *in situ* on sandy beaches using the M-BACI design in order to analyse the effect of this manipulation on macroinvertebrate species such as *T. saltator*. The results of the M-BACI experimental model indicated that differences in the patterns of change between the impacted and control plots were related to the effect of the removal of stranded wrack on *T. saltator* density, since no differences between treatments were found for densities values before this disturbance. This effect was manifested as decreased in the densities of *T. saltator* associated with wrack patches in comparison to control plots, although the evidence of significant effects was different at each beach studied.

The removal of organic beach cast materials along the driftlines is assumed to be a source of disturbance for talitrid amphipods, such as *T. saltator*, because of the reduction of organic matter available and the loss of suitable microhabitat for amphipods (Dugan et al., 2003; Fanini et al., 2005; Gilburn, 2012; Bessa et al., 2014a). For this, we designed a field experiment to evaluate only the effect of a single source of disturbance (i.e. wrack removal) on strandline *T. saltator* density at two natural and ungroomed beaches, in order to isolate that disturbance. Moreover, the applied M-BACI design enabled us to quantify the temporal extent of the effect of this disturbance on *T. saltator* density. Our experiment is the first direct proof that wrack biomass removal activity diminishes the density of *T. saltator* associated with the stranded wrack ungroomed upper shores. This effect could be significant at managed beaches, due to all debris (human-generated debris, carrion, seagrass, macroalgae, etc.) are indiscriminately removed by grooming practices, damaging macroinvertebrates populations, such as talitrid amphipods, associated with wrack debris. It is important to take into account that the effect of this disturbance was tested on spatial scale (~ 100 m along upper shore) which is probably not the same as in management practices (i.e. cleaning, harvesting, etc.) on sandy beaches. However, this study attempts to evaluate whether the temporally suppression of wrack debris could affect the density of a highly abundant species associated with wrack debris, such as *T. saltator*.

We expected a stronger influence of the wrack removal on *T. saltator* densities, given the role of stranded wrack as shelter and/or food source for talitrid amphipods (Lastra et al., 2008; Olabarria et al., 2009; Gonçalves and Marques, 2011; Bessa et al., 2014a). However, in our study this disturbance did not appear to be severe enough to drastically change their densities at the strandlines, probably due to organism's capacity to withstand stressful events (Scapini 2006, 2014). In this sense, we found a decline in

density of *T. saltator* in the impacted plots on Levante beach, immediately after the period of wrack removal. However, the recovery to the pre-impact population level was fast and the recolonization was complete between the third and the sixth day after the wrack removal, as shown by the higher total density in impacted plots than in the same plots before the disturbance on Levante beach. This response pattern could be defined as a "pulse" disturbance, i.e. a short-term effect with a sudden drop in density followed by a rapid recovery in the absence of new disturbances (Glasby and Underwood, 1996). Moreover, total density of *T. saltator* changed weakly between impacted plots and control plots immediately after the disturbance at Cortadura beach. The observed responses of *T. saltator* density might be related to the mobility and burrowing abilities of *T. saltator*. It is possible that, during the wrack removal, individuals avoided this disturbance by burrowing deeply into the surrounding sand or by displacing to a safer and undisturbed zone such as foredunes (Llewellyn and Shackley, 1996) or unmanipulated plots. In any case, it seems that *T. saltator* individuals are able to recolonize strandlines after the disturbance, when new algal wrack deposits became available. These results suggest the ability of *T. saltator* to withstand a removal of wrack debris, at the spatial and temporal scaled used in this study, at the sandy upper beaches. However, studies on the surface activity of *T. saltator* are needed to explain the mechanisms contributing to the effect of wrack removal on *T. saltator* populations.

The different responses of *T. saltator* at the two beaches studied could also be related to morphodynamic state and the specific composition of stranded wrack on each beach. During the experiment, the mean density of *T. saltator* was higher in wrack debris at Cortadura than at Levante beach. This difference was probably explained by the morphodynamic state of each beach. According to the habitat safety hypothesis (Defeo and Gomez, 2005) the abundance of talitrid amphipods in the supralittoral zone of an intermediate beach (Cortadura) is higher than in a dissipative beach (Levante). Moreover, Lastra et al. (2008) reported that the amount and also the composition of wrack deposits can limit the density of beach consumers such as *T. saltator*. It is possible that stranded seagrasses occurring in the strandline at Levante beach can attract fewer *T. saltator* individuals than does the drifting macroalgae at Cortadura beach. This is in line with McMillan and Quijon (2012), who found that the number of macrofaunal organisms, mainly talitrid amphipods, proved higher on stranded macroalgae patches than on eelgrass patches. Previous studies have reported that *T. saltator* does not feed directly on seagrass leaves (Adin and Riera, 2003; Colombini et al., 2009), so that its

abundance in seagrass deposits could be low because of the possible need to forage on other food sources (e.g. dune plants, particulate organic matter, carrion, etc.) at the foredunes and/or the midlittoral zone. A recent study has demonstrated the ability of *T. saltator* to change the foraging habitat (foredunes or intertidal) in relation to the availability of allochthonous resources along the sea-dune axis, particularly on sandy shores with a low contribution of seaweeds in the strandline (Bessa et al., 2014a). However, the high availability of stranded macroalgae (mainly brown algae) at Cortadura beach could concentrate *T. saltator* individuals on wrack deposits searching for food, since brown algae are the preference food source for *T. saltator* (Adin and Riera, 2003; Olabarria et al., 2009) as well as others food items available near to wrack deposits on a highly subsidized beach (Bessa et al., 2014a). All of these reasons might explain the higher density of *T. saltator* associated with wrack patches at Cortadura than Levante beach and, consequently the less response of this amphipod in the former than the latter beach related to the removal of algal wrack.

Differences in the life stage of amphipods appeared in the response pattern of adults and juveniles. The density of juveniles was lower in impacted than in control plots after the wrack removal, particularly on Levante beach, whereas the density of adults remained similar in both treatments. This result could be related to intrinsic differences in the behaviour and physiological needs between the two age classes (Fallaci et al., 1999, 2003; Scapini et al., 1992; Scapini, 1997; Williams, 1983). For example, juveniles are unable to burrow as efficiently as adults and are usually recorded more superficially burrowed below wrack deposits (Williams, 1995). Moreover, juveniles are more active than adults in searching for decayed beach debris, because they are more susceptible to dehydration than adults (Williams, 1983). This could also be related with their different diets. Colombini et al. (2011) reported that juveniles show higher proportions of allochthonous marine components in their diet than do adults, which can feed on other food items. Therefore, juveniles could be more sensitive to wrack removal, due to their dependence on wrack debris. On the other hand, the different response patterns of adults and juveniles may also reflect their difference in size. Smaller individuals have relatively reduced locomotion and thus cannot move as far as adults can (Scapini et al., 1992; Scapini, 1997). This may explain the lower impact on the density of adults after the wrack removal on both beaches.

In summary, this study is the first experiment which manipulated wrack biomass in two sandy beaches using the M-BACI design. Our experimental approach

demonstrated that *T. saltator* may be resilient, withstanding short-term disturbances associated with wrack removal activity or quickly recovery after this disturbance. Juveniles appear to be more sensitive to this disturbance than adults, although this pattern apparently depends on the density of individuals associated with wrack debris at each beach studied. The amount and composition of wrack debris can influence on the density of wrack associated fauna, such as *T. saltator*, and, therefore, a pulse disturbance in driftlines may not always have the same effect on a particular species.

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GENERAL DISCUSSION

GENERAL DISCUSSION

Wrack deposits are a distinctive feature of sandy beaches worldwide and a potential resource for resident invertebrate communities, particularly those living on the upper beach, and for terrestrial vertebrates such as shorebirds, reptiles, and amphibians linked to wrack (e.g. Dugan et al. 2003; Ince et al. 2007; Spiller et al., 2010; MacMillan and Quijón, 2012; Lafferty et al., 2013). The stranding of wrack debris is considered a small-scale physical disturbance increasing habitat heterogeneity, which explains the association of supralittoral macroinvertebrates with wrack debris (e.g. Dugan et al. 2003; Jaramillo et al., 2006; Ince et al. 2007; MacMillan and Quijón, 2012). However, the spatial variation of wrack and the potential influence of its habitat features on upper-shore beach organisms remain poorly understood. Despite that strandlines can support rich supralittoral fauna of crustaceans and insects, which can be found in no other environment (Colombini and Chelazzi, 2003) and play key roles in the ecosystem functioning (e.g. Jędrzejczak, 2002b; Mews et al., 2006; Dugan et al., 2003; Lastra et al., 2008; Gonçalves and Marques, 2011), wrack debris is removed from sandy beaches worldwide. However, the direct effects of wrack removal on invertebrate assemblages have not been evaluated. This thesis attempts to understand the spatio-temporal variations in wrack-associated fauna in relation to the spatial distribution and the habitat features of stranded wrack debris, as well as the consequences of its removal on strandline assemblages. The results of this work contribute to a better understanding of the relationships between supralittoral invertebrates and wrack debris, which is essential to improve the management of this key component on sandy beaches.

- **Macroinvertebrates associated with wrack debris: spatial and temporal patterns**

The amounts of allochthonous subsidies (i.e. wrack debris) on any beach depend on the production of the adjacent habitats, physical beach environment (e.g. rate of exposure, beach slope, wave height, type of substratum), and the composition and buoyancy of the drifting wrack (Ochieng and Erftemeijer, 1999; Orr et al., 2005; Barreiro et al., 2011; Duong and Fairweather, 2011). Therefore, high variability in the amount of stranded wrack (i.e. standing crop) was detected on sandy beaches of southern Brazil and south-western Spain (**Chapter 1**). It appears that some of this variation was related to different morphodynamic states of beaches, which differed with the position of the

beaches on the coast. Thus, beaches with low wave heights, high RTR values, and gentle slopes showed the highest standing crop. These features could create favourable conditions for stranding wrack, as suggested by Barreiro et al. (2011). Moreover, the proximity of beaches to donor ecosystems such as mangroves, rocky intertidal areas, and rocky shores could influence the standing crop on beaches studied, as previous studies have reported (e.g. Ochieng and Erftemeijer, 1999; Dugan et al., 2003; Barreiro et al., 2011).

Wrack deposits are the major source of temporal and spatial habitat heterogeneity which influence the structure of supralittoral macroinvertebrates (Inglis, 1989; Colombini et al., 2000; Jedrzejczak, 2002a; Gonçalves and Marques, 2011). Our results reveal that supralittoral assemblages were associated with different types of stranded organic materials, i.e. macrophytes, macroalgae, mangrove propagules, and carrion in Atlantic sandy beaches of southern Brazil and south-western Spain (**Chapter 2**). These assemblages were composed of talitrid amphipods followed by tenebrionid and/or staphylinid coleopterans, which accounted for approximately 80% of the communities. Previous studies have reported high abundance of talitrids and coleopterans (i.e. Tenebrionidae and/or Staphylinidae) in beach-cast macroalgae of sandy beaches worldwide (Lavoie, 1985; Colombini et al., 1998, 2000; Dugan et al., 2003; Jaramillo et al., 2006; Olabarria et al., 2007). However, this is first time that the composition of macroinvertebrates associated with other types of wrack debris is analysed, apart from algae wrack.

The species diversity and density of these macroinvertebrates were demonstrated to be higher in wrack patches than in nearby bare areas on two sandy beaches of the south-western Spanish Atlantic coast (**Chapter 2**). This result is consistent with previous studies which have demonstrated that wrack patches enhance the number of species and abundance of supralittoral arthropods (Dugan et al., 2003; Jaramillo et al., 2006; Ince et al., 2007; Rodil et al., 2008; MacMillan and Quijón, 2012). At the community-level, analyses have shown that the composition and structure of supralittoral assemblages differed between wrack-covered and uncovered areas on both Spanish Atlantic beaches. Thus, several species (belonging to different groups, such as talitrid amphipods, tylid isopods, coleopterans, dipterans, arachnids, etc.) were associated with wrack debris, but no species were encountered exclusively on sand devoid of wrack. This pattern was clearer in summer than winter, since the summer is the season with the highest abundance of macrofauna (Behbehani and Croker 1982;

Gonçalves and Marques, 2011; Dufour et al., 2012). Particularly, Talitridae (*Talitrus saltator*), Tenebrionidae (adults of *Phaleria bimaculata* and larvae of this family), and Staphylinidae (e.g. *Cafius xantholoma*, *Remus sericeus*, *Carpelimus rivularis*) species were more abundant in wrack patches than on bare sand, where these were practically absent (e.g. tenebrionids and staphylinids species) or present in very low abundances (e.g. talitrids). Several studies have indicated that algal wrack debris represent the main food resource for upper-shore detritus feeders such as talitrid amphipods, oniscoid isopods, tenebrionids, and staphylinids (Dugan et al., 2003; Ince et al., 2007; Lastra et al., 2008; Colombini et al., 2011a; Bessa et al., 2014). Furthermore, beach-cast marine algae can be used as a refuge from desiccation by supralittoral macroinvertebrates (Jaramillo et al., 2006; Olabarria et al., 2007; McMillan and Quijón, 2012), providing an opportunity to study seaweed debris either as shelter and/or feeding sites. The results of **Chapter 2** indicate that the labile organic matter (i.e. biopolymeric carbon fraction, BPC) combined with temperature or moisture explained the association of arthropod assemblages with wrack deposits during summer on the two Spanish Atlantic beaches. This result suggests that wrack deposits offer more hospitable conditions than does bare sand, considering microclimatic factors and food availability, which structure diversity and composition of supralittoral arthropods.

On the upper beach, wrack can be deposited along one or more drift lines, usually at high water spring line and in bands or in a band down to the level of the most recent high tide (Marsden 1991, Ochieng and Erftemeijer, 1999, Colombini et al., 2000). Such distribution patterns affect the abundance and distribution of supralittoral macroinvertebrates, mainly detritus feeders (e.g. Stenton-Dozey and Griffiths, 1983; Jaramillo et al., 2006; Rodil et al., 2008). Our results show that the distribution of wrack debris in bands had an effect on the structure of supralittoral assemblages in most of the study beaches of southern Brazil and south-western Spain (**Chapter 1**). This influence was detected in the density of the most abundant taxa: talitrid amphipods dominated lower wrack bands, located at the most recent driftline and composed of newly stranded material, while staphylinid and tenebrionid species occupied upper wrack bands, located above the recent driftline and composed of dried and aged material. However, in this study only the relative age of wrack deposits, which differ in their position in the supralittoral zone, was used as the explanatory variable of the distributional patterns of species. This result was complemented with the results of **Chapter 2**, in which specific features such as microclimatic conditions (i.e. temperature and moisture), food

availability, and nutritional quality were measured in wrack debris on the two Spanish Atlantic beaches. Previous studies have indicated that the distribution patterns of arthropods along supralittoral areas may depend on the preference for specific microhabitats and/or food sources that differ according to resource requirements of the different species (Colombini et al., 2000; Pennings et al., 2000; Jaramillo et al., 2006; Colombini et al., 2011a). Our results demonstrated that the habitat features (microclimatic conditions and food nutritional quality) changed with the position of wrack deposits (i.e. their relative ageing). The moisture availability and/or the nutritional content of wrack bands explained the distributional pattern of talitrid amphipods, tenebrionid, and staphylinid species between these wrack bands at both Spanish Atlantic beaches. The results of both chapters provide evidence concerning the role of wrack debris in shaping diversity and composition of supralittoral arthropods, stressing the importance of the habitat heterogeneity to maintain abundant and diverse communities on supralittoral zone of exposed sandy beaches.

Focusing on the temporal variability of wrack debris and their associated communities, we performed manipulative experiment to analyse the colonization process in natural strandlines (i.e. wrack washed ashore at the supralittoral zone) (**Chapter 3)**. Previous studies have evaluated the colonization and successional dynamic in wrack patches (Lavoie, 1985) or using litterbags (Inglis, 1989; Jędrzejczak, 2002b; Dufour et al., 2012) or artificial algal patches (Olabarria et al. 2007; Garrido et al., 2008; Rodil et al., 2008) during the decay of organic matter, but this process has not been previously evaluated in natural strandlines. Most of these studies reported talitrid amphipods and dipterans as primary colonizers of algal patches, while different insect species, mainly coleopterans (e.g. staphylinids, tenebrionids, ptiliids, histerids, etc.) and spiders, are deemed late colonizers (i.e. few days after the initial wrack deposition). Nevertheless, natural strandlines are highly variable, because the specific habitat attributes of wrack debris change temporally as these undergo the dynamics of the beach environment (i.e. stranded and ageing or re-deposited and re-exposed in successive tides). Therefore, natural strandlines are composed by wrack patches with different stages of ageing (i.e. from new fresh materials to dry, decomposed materials) patch sizes, etc., which can expand the range of habitats and food sources available for supralittoral arthropods. Our results (**Chapter 3)** demonstrate that a wide range of colonizer species (such as talitrid, dipterans, tenebrionids, staphylinids, and spiders) were found in wrack debris from the first three days after the stranding of natural wrack

debris. This pattern was detected in the sandy beaches of the Atlantic coast of southern Brazil and south-western Spain.

The colonization of strandlines by upper-shore arthropods was quick (within a 3-day-period) in sandy beaches subsidized by algae wrack (i.e. south-western Spain). The same time period (i.e. 3 days) of colonization has been previously reported in artificial algal wrack patches (Inglis, 1989; Olabarria et al., 2007; Rodil et al., 2008; Dufour et al., 2012). Notably, the colonization of natural wrack debris was slower (i.e. within a 16-day period) in the Paraná region. This study is the first to report on the colonization process in wrack debris naturally stranded, such as mangrove propagules, on subtropical beaches. Our results suggest that the dynamic of wrack biomass, as well as the species-specific adaptations (i.e. mobility) and strategies to use wrack debris (i.e. as refuge and/or feeding sites) by some taxa such as talitrid amphipods and coleopterans (clerids and nitidulids in Paraná region and tenebrionids and staphynilids in both regions) could explain the different colonization patterns of supralittoral assemblages in Atlantic sandy beaches of Brazil and Spain. This study reveals the ability of supralittoral macroinvertebrates to colonize natural wrack debris washed ashore on the upper beach of both Atlantic regions. Knowledge of the colonizing ability and the temporal changes of species associated with wrack debris is key for evaluating the potential responses of macroinvertebrate assemblages to changes of the supralittoral environment. More broadly, this information can be relevant to propose management measures of wrack debris for adequate conservation.

- **Wrack removal as disturbance for supralittoral arthropods: from the community to the populations associated with wrack debris**

The availability of wrack debris is reported as the main factor structuring supralittoral communities (Ochieng and Erftemeijer, 1999; Dugan et al., 2003; Gonçalves and Marques, 2011). The results of previous chapters (1 and 2) of this thesis demonstrate the influence of wrack deposits on the structure of supralittoral communities, because wrack debris is used as a food source and/or refuge from environmental conditions. Therefore, the temporal suppression of the stranded wrack biomass on the upper shores may affect community structure and composition. Although the removal of wrack debris along the driftlines is assumed to be a source of disturbance for strandline-associated fauna because of the loss of shelter as well as breeding and/or feeding sites (e.g. Dugan et al.,

2003; Gilburn, 2012), no experimental field studies have shown the direct effect of the the wrack-biomass reduction on macroinvertebrate assemblages at the strandlines. Therefore, manipulative experiments were performed to evaluate *in situ* the direct effect of wrack removal on associated assemblages. The M-BACI design was used, for the first time, to analyse the response patterns of the whole community (**Chapter 4**) and of some target species (i.e. talitrid amphipods) after the wrack removal (**Chapter 5**). The results of **Chapter 4** reflect that the significant reduction of wrack biomass after the removal activity corresponded with structural shifts in assemblages over the short term (days to weeks), although the period of time in which the effects were measurable varied in each Atlantic region (southern Brazil and south-western Spain). In the Paraná region (southern Brazil) changes in the overall community structure were detected between 3 to 16 days after the disturbance. These changes were attributed to the declines in the total density of the amphipod *Platorchestia monodi* and the coleopterans Cleridae and Nitidulidae followed by a quick recovery of their densities in the disturbed areas after the wrack removal. In SW Spain, temporal differences were detected within the first three days after the disturbance related to the reduction of total density of the amphipod *T. saltator*. Our results suggest that supralittoral macroinvertebrates are able recover their densities after the removal of wrack debris in the absence of new disturbances (i.e. pulse disturbance) in both regions. The significant and continuous stranding of wrack debris (i.e. standing crop) on the beaches during the experiment could promote a quick recovery of the communities inhabiting strandlines after the removal of debris as a previous study reported for talitrid amphipods after the clean-up activities in estuarine beaches (Borzone and Rosa, 2009). Moreover, this rapid recovery could be related to the fact that naturally stranded wrack debris can be promptly invaded (within the first three days after its stranding) by a wide range of colonizer species (e.g. talitrid, dipterans, tenebrionids, staphylinids, and spiders) as demonstrated in the sandy upper beaches of both Atlantic regions (Chapter 3). Therefore, it is possible that the active migration to and concentration of organisms at local sites without wrack, such as dunes or vegetated backshores, during the cleaning activity, may contribute to the maintenance and posterior subsequent increase in species densities in the disturbed areas when wrack debris becomes available on the upper shores. However, it is possible that regular cleaning events on a greater time scale (e.g. months) might induce more protracted recovery of the communities than would a short-term cleaning event. Field experimental studies are needed to test this hypothesis.

It is interesting to notice that the removal of wrack debris trigger declines in the densities of talitrid amphipods (*P. monodi* and *T. saltator*) in the disturbed areas, but *T. saltator* recovered more quickly (3 days) than did *P. monodi* (between 6 to 16 days). This result suggested that the two species could show differ in behavioural strategies (e.g. burrowing abilities, mobility, etc.) to cope with the same disturbance at the upper driftlines. In the case of *T. saltator*, besides the effect on the total density, the effect was analysed on the density of juveniles and adults on the two Spanish Atlantic beaches (**Chapter 5**). The density of juveniles was lower in the disturbed than in the control plots three days after the wrack removal, particularly on Levante beach, whereas the density of adults remained similar in both treatments at both beaches (Levante and Cortadura) over time. The inability to burrow, the reduced mobility, the high susceptibility to dehydration, and the use of marine subsidies as the major food source for juveniles (Williams, 1983; Scapini et al., 1992; Scapini, 1997; Colombini et al., 2011a) could explain the greater sensitivity of juveniles to wrack removal than adults. Previous studies have demonstrated that other types of pulse disturbance such as ORV traffic or trampling, cause significant reductions in burrow densities and structure size of other crustaceans such as ghost crabs (Schlacher and Lucrezi 2010; Lucrezi et al., 2009a), which are commonly used as bioindicators of environmental disturbances on sandy beaches (e.g. Lucrezi et al., 2009b; Noriega et al., 2012; Schlacher et al., 2011). However, few experimental studies have examined human disturbance of supralittoral fauna on sandy beaches, this dearth of information precluding more robust conclusions. Therefore, experimental studies are necessary to understand the mechanisms provoking the impact on supralittoral populations, since management intervention should target the processes that cause the actual impact on the macroinvertebrates.

The removal of wrack debris in supralittoral zones can change the available nutrient pools for supralittoral macroinvertebrates and thereby compromise the connection between wrack-associated fauna and the rest of trophic food web of these boundary systems, jeopardizing the ecological functioning of the entire beach ecosystem. The lack of information regarding the wrack debris as harbouring macroinvertebrate diversity and providing habitats and/or food as well as the effects of the reduction of wrack biomass on associated macroinvertebrates, could limit an accurate evaluation of the ecological functioning of wrack debris on sandy beaches. This information is relevant in conservation and management plans, which should consider wrack a key component in coastal ecosystems (Duarte et al., 2004; Schlacher

et al. 2014). For this, it is important to inform the public that natural stranded debris should not to be considered litter and should be left on beaches because it is essential for the ecosystem (e.g. Fairweather and Henry, 2003; Colombini and Chelazzi, 2003; Dugan et al., 2003; Defeo et al., 2009, Dugan and Hubbard, 2010; Barreiro et al., 2013; Schlacher et al. 2014). In Northern Europe, campaigns of environmental education (information leaflets, panels, etc.) have proved to be effective and people have become more sensitive to environmental issues (Von Rohr et al. 2008). In fact, a public-perception study about the beach user's opinion on beach cleanliness in Belgican beaches indicated that manual beach cleaning was supported by 75% of beach users, who agreed that the natural drift-line material was neccesary and should not be removed from beaches (Domínguez and Belpaeme, 2006). Therefore, such campaigns should be conducted in coastal regions worldwide in order to raise awareness concerning the importance of this key component (i.e. wrack debris) for beach ecosystems. Moreover, it could be useful to assess the thresholds of organic debris that beachgoers consider to as reaching the nuisance levels (Duarte, 2004). It is possible that not all beach users consider natural debris a nuisance that to be removed from beaches anywhere (Colombini et al., 2011b). Ideally, these efforts would result in reduced pressure by users to have the beach-cast materials removed. Finally, the cleaning of beaches could be approached in an environmentally responsible way.

This thesis increases our knowledge concerning the interaction between wrack debris and supralittoral macroinvertebrates, highlighting the role of stranded organic materials in shaping communities as shelter, breeding and/or feeding sites. Moreover, the results of this study demonstrate that the removal of wrack debris affect the structure and composition of supralittoral assemblages. Therefore, wrack debris should be considered a key component on sandy beaches because it provides habitat and food for supralittoral macroinvertebrates, forming islands of biodiversity which support coastal food webs. The conservation of wrack debris and the reduction of human impact on associated fauna are crucial to maintain the functional integrity of beach ecosystems.

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CONCLUSIONS

CONCLUSIONS

1. High variability was detected in the standing crop (i.e. wrack biomass) among beaches in the three study regions of Brazil and Spain. This spatial variability was likely related to the different morphodynamic states of the beaches, which are influenced by their position on the coast. Thus, the beaches with low wave heights, high RTR values, and gentle slopes showed the highest standing crop in each region. Moreover, the variability in the amount of wrack between beaches could be related to the proximity of these to the source of allochthonous organic materials such as mangroves, rocky intertidal areas, and rocky shores in each region.

2. Different types of wrack deposits, i.e. seagrasses, macroalgae, mangrove propagules, and macrophytes, provide a physical structure which can be used as shelter, breeding and/or feeding sites for supralittoral arthropods on Atlantic sandy beaches of Brazil and Spain. These assemblages were composed mainly of talitrid amphipods, tenebrionids, and/or staphylinids species, which accounted for approximately 80% of the communities.

3. Wrack deposits enhance the number of species and abundance of supralittoral arthropods. Several species belonging to different groups, such as talitrid amphipods, tylid isopods, coleopterans, dipterans, and arachnids, were associated with wrack debris, but no species were encountered only on sand devoid of wrack on the two Spanish Atlantic beaches.

4. The association of invertebrates with wrack was explained by the labile organic matter (i.e. biopolymeric carbon fraction, BPC) combined with temperature or moisture underneath wrack patches on the two Spanish Atlantic beaches. Therefore, our results demonstrated that wrack deposits offer more hospitable conditions than does bare sand, considering microclimatic factors and food availability, which influenced the structure and composition of supralittoral arthropods.

5. The distribution of wrack debris in bands had an effect on the structure of supralittoral assemblages in most of the Atlantic beaches studied of Brazil and Spain. Wrack debris position affected the density of the dominant taxa such as

talitrid amphipods, tenebrionids, and staphylinids. Talitrid amphipod species were associated with fresh wrack bands, located at the most recent driftline, while staphylinids and tenebrionids occupied aged wrack bands, located above the recent driftline.

6. Our results showed that upper wrack bands were characterized by high temperature, low moisture, and a low protein-to-carbohydrates ratio, while lower wrack bands presented the opposite features, related to the different state of dehydration and ageing of each band. The differences in habitat features explained the segregation of talitrid amphipods and coleopteran (i.e. Tenebrionidae and Staphylinidae) species between wrack bands on the supralittoral zone of two Spanish Atlantic beaches.

7. The colonization of natural wrack accumulations did not occur in a predictable pattern (i.e. early to late), but instead species of different stages of succession (i.e. early, middle, and late) colonised wrack debris from the first three days after the stranding of natural wrack debris.

8. The colonization of natural strandlines was slower in southern Brazil (16-day period) than in south-western Spain (3-day period). This process was driven by changes of the densities of Talitridae, Staphylinidae, and Tenebrionidae species associated with wrack debris in both regions. The dynamics of wrack biomass, the species-specific adaptations (i.e. mobility), and the strategies to use wrack debris as refuges and/or feeding sites seem to influence the colonization patterns of supralittoral assemblages in both Atlantic regions (Paraná and SW Spain).

9. The significant reduction of wrack biomass after the removal activity corresponded to changes in the structure of supralittoral assemblages over the short-term (days to weeks) on sandy beaches of both Atlantic regions (Paraná and SW Spain). While in Paraná region these changes were attributed to the declines in the total density of the talitrid amphipod (*Platorchestia monodi*) and the coleopterans Cleridae and Nitidulidae associated with wrack debris, in south-western Spain region these were attributed to the reduction of the total density of the amphipod *Talitrus saltator*. The short-term effects suggested that supralittoral fauna might exhibit behavioural strategies (e.g. rapid burrowing, escape responses, high mobility, etc.) to avoid the negative effects of the wrack

removal, occupying disturbed areas when wrack debris became available on the upper shores.

10. Talitrid amphipods showed declines in density (nº ind./ m^2 of the surface covered by wrack) after the removal of wrack debris. However, *Talitrus saltator* recovered in disturbed areas more quickly (in 3 days) than did *Platorchestia monodi* (between 6 to 16 days). This result demonstrated the different ability of talitrid species to recover in strandlines on the upper beach after a short-term disturbance. Comparative studies on the behavioural strategies of these key species should be performed to understand their response patterns after a disturbance on the sandy upper shores.

11. *Talitrus saltator* may be resilient, withstanding short-term disturbances associated with wrack removal or quickly recolonizing manipulated sites after the removal activity. Juveniles appear to be more sensitive to this disturbance than are adults, although this pattern apparently depends on the density of individuals associated with wrack debris at each beach type (intermediate or dissipative). Moreover, the amount and composition of wrack debris can influence the density of wrack-associated fauna, such as *T. saltator*, and, consequently, the response pattern after wrack removal. Therefore, a pulse disturbance in driftlines may not always have the same effect on a particular species.

12. Over the short-term, the wrack removal acted as a pulse disturbance: i.e. a short-term decline on species densities followed by a rapid recovery in the absence of new disturbances. This suggests that supralittoral fauna can be resilient to temporal variability of the wrack supply.

13. This thesis demonstrates the role of wrack debris in shaping communities and the influence of its habitat features on the spatial distribution of supralittoral macroinvertebrates. Moreover, the temporal variability of strandlines determined the structure and composition of colonizer communities of wrack debris in sandy upper beaches. The removal of wrack debris disrupted the structure and composition of supralittoral assemblages and lowered the density of some key species such as talitrid amphipods. In general, the short-term wrack removal is demonstrated to be a disturbance of the composition and structure of

macroinvertebrates inhabiting strandlines on exposed Atlantic sandy beaches. In essence, this work highlights wrack debris as a source of habitat and species diversity. Therefore, wrack debris should be considered as key component in the conservation and management plans of beach ecosystems.

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